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TULANE STUDIES IN ZOOLOGY AND BOTANY

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A REVISION OF THE MIDDLE AMERICAN THECOPHYLLOID VRIESEAS (BROMELIACEAE)

JOHN F. UTLEY

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A Revision Of The Middle American Thecophylloid Vrieseas (Bromeliaceae)

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Abstract

The thecophylloid vrieseas were long maintained in a distinct genus, *Thecophyllum*, because of their enlarged primary bracts and reduced secondary inflorescence branches. These taxa currently form a geographically and morphologically cohesive alliance within section *Xiphion* of *Vriesea*. In addition to the nocturnal flowers generally encountered in section *Xiphion* several thecophylloid vrieseas display crepuscular and diurnal anthesis and floral syndromes suggestive of adaptation to a wide range of pollen vectors. Keys, descriptions and synonymies are provided for the Middle American taxa and their relationships are discussed. *Vriesea greenbergii, V. kathyae, V. luis-gomezii* and *V. lyman-smithii* are illustrated and described as new species.

Introduction

The genus *Thecophyllum* was described by Andre, on the basis of enlarged primary bracts and aborted lateral inflorescence branches. His treatment included two species, *Thecophyllum poortmanii* André and *T. wittmackii* André. In 1896 Mez reduced *Thecophyllum* to a section of *Guzmania* and included 14 species in the new section. Mez (1903a) reinstated *Thecophyllum* at the generic level and transferred the 14 species from his section to the renovated genus; he concomitantly emended André's original description to include species with enlarged primary bracts, aborted or highly reduced secondary inflorescence branches and free, appendaged petals. Mez's action resulted from the opportunity to study additional material of *Guzmania ororiense* Mez from Costa Rican collections of Pittier. During the following 13 years Mez (1903-1916), added a number of species to *Thecophyllum*, so that when he treated the Bromeliaceae in Das Pflanzenreich (1934-1935), *Thecophyllum* contained 45 species. Smith (1932, 1938) described four new species in *Thecophyllum*, and Suesenguth and Goeppinger (in Suesenguth, 1942) added two species and a variety, bringing the total number of species in the genus to 51. Smith and Pittendrigh (1953) transferred all *Thecophyllum* species to *Guzmania, Tillandsia* or *Vriesea*. The two species considered by André when he originally established the genus and 11 other species were relegated to *Guzmania*, two species were transferred to *Tillandsia* and the vast majority (38) of the taxa were transferred to *Vriesea*, where they were placed in section *Xiphion*.

Those species transferred to *Vriesea*, as well as several species named as vrieseas since 1953, form a homogeneous group within section *Xiphion*. These thecophylloid vrieseas are more than 80% endemic to Costa Rica and Western Panamá. Within this area they are largely confined to the moister parts of the lower montane, premontane and montane regions. They are separated from the remainder of sections *Xiphion* by the same characteristics which distinguished *Thecophyllum* sensu Mez reduced lateral inflorescence branches and enlarged primary bracts. Moreover, the thecophylloids are distinguished from the majority of vrieseas by a unique stigmatic morphology that they share with a group of low to middle elevation members of the section *Xiphion*. The vrieseas, like the thecophylloids, are highly diverse in Middle America.

Habitat And Ecology

From my extensive field work in Costa Rica. I interpret that the ecological dis-

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tribution of most thecophylloids exhibits a positive correlation with the life zone classification developed by Holdridge et al. (1971). The elevational distribution of the thecophylloids is confined to the area between 300 and 3200 m, while the vast majority of species are found between 900 and 2100 m (Fig. 1). Within this elevational range the taxa are confined to five life zones; premontane rain forest and wet forest, lower montane rain forest and wet forest, and montane rain forest.

Most thecophylloid vrieseas are restricted to one or two life zones. When a species occupies more than two life zones, the extension occurs into life zones that border on the principal one (s). Alternatively, species may occur in the center of an additional life zone, but this is invariably in conjunction with an isolated peak or ridge system that is regularly exposed to cloud and mist conditions. For terrestrial vegetation the general life zone of such exposed elevations may be a "wet zone" in the Holdridge system, but the additional atmospheric moisture present in mist and clouds effectively makes the epiphytic habitat equivalent to a "rain zone."

A prime example of this situation is the crest of the Cedral or Cerros de Escazu, located south of San Jose, Costa Rica. This chain is located in the lower montane wet formation of Holdridge, but the crest and peaks of this chain receive almost daily clouds and mist. The area is an extremely rich collecting location for *Vriesea nephrolepis*, a species common in the lower montane wet forest life zone. However, near the crest of this range, and in particular crests of the individual peaks, *V. ororiensis* and *V. williamsii*, species typical of the montane and lower montane rain forest life zones, are common. These taxa are further stratified; *V. williamsii* is found only within a few yards of the peaks, whereas *V. ororiensis* is common in a narrow band below the crest. This distribution apparently parallels subtle changes in the availability of atmospheric moisture. This assumption is reinforced by my observations from field and horticulture that indicate that *V. williamsii* exhibits less tolerance for desiccation than *V. ororiensis*. The extension of these two species into a drier life zone is undoubtedly facilitated by the regular availability of atmospheric moisture.

Anomalies in the life zone system due to cloud and mist drift were predicted by Holdridge (1967), and Walter (1971) mentioned that epiphytes are good indicators of microclimatic factors such as ambient humidity. Moerover, Pittendrigh (1948) related moisture requirements of bromeliads to their distribution in Trinidad. The phenomenon was discussed for bromeliads in particular by Gilmartin (1973) who concludes that knowledge of bromeliad distribution in conjunction with a physiognomic-ecological classification (e.g. the Holdridge Life Zone System) might be effectively used to indicate vegetational types. I agree with Gilmartin's findings, but, I feel that use of epiphyte distribution might be better described as a "fine tuning" of the life zone system. Knowledge of epiphyte distribution in conjunction with the life zone system allows one to infer conditions of atmospheric moisture or seasonal variation in precipitation that are not reflected in general vegetational structure.

As previously mentioned the thecophylloids are highly endemic to Costa Rica. All species found in Central America are also found in Costa Rica. Three species native to Costa Rica extend northward as far as Honduras, and one of these extends into southern México. *Vriesea pedicellata* is common in the Cordillera Central of Nicaragua and has been collected as far north as Montaña Uyuca in Honduras. *Vriesea nephrolepis* extends into Guatemala and *V. hygrometrica* has been collected at Vista Hermosa in the state of Oaxaca, México. The southeastern extension of thecophylloids into Panamá

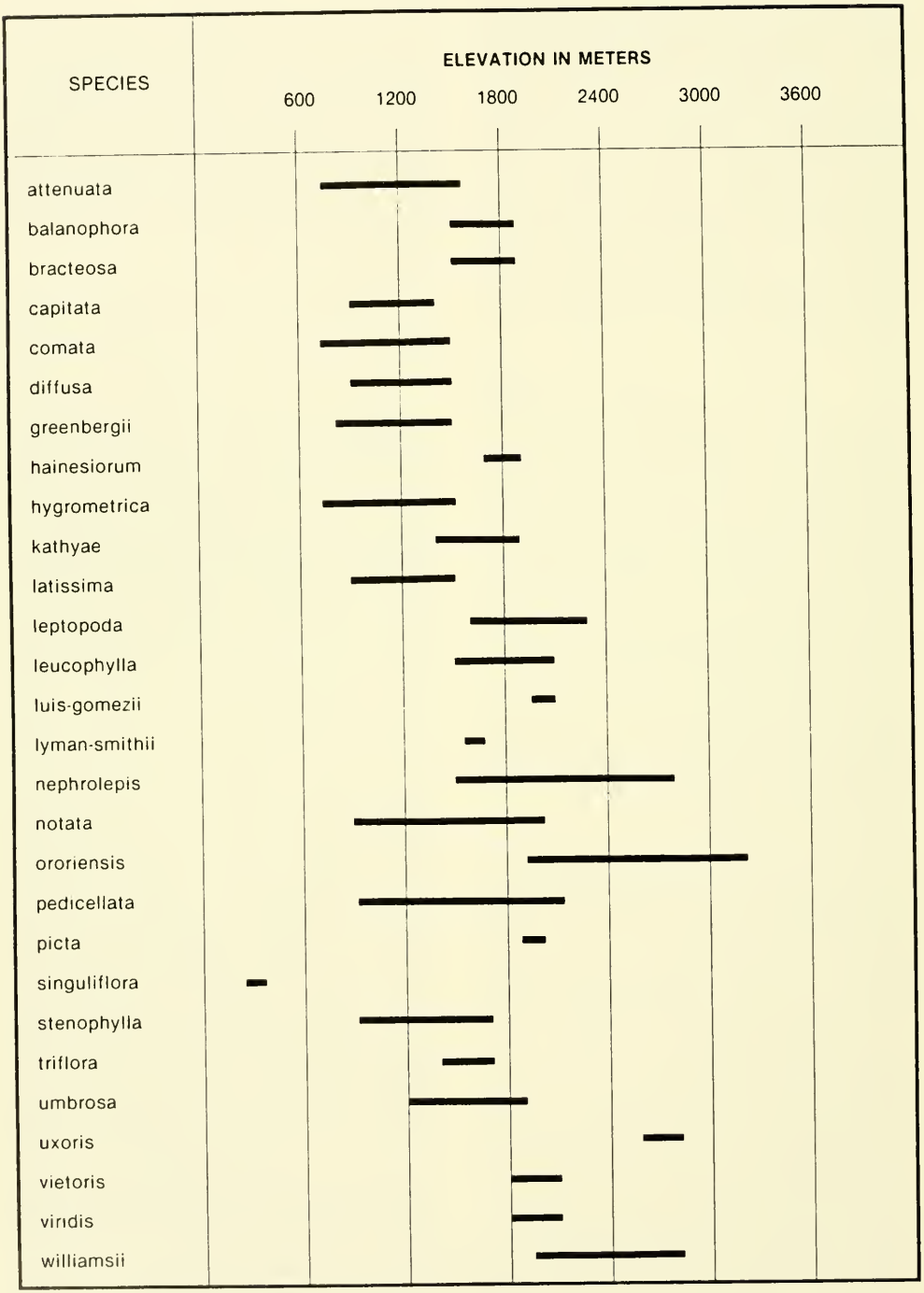


Fig. 1. Elevational ranges of thecophylloid vriesea species in Middle America.

is to be expected considering the phytogeographic continuum provided by the Cordillera de Talamanca which extends into central Panamá. Several species, *Vriesea leptopoda, V. leucophylla, V.ororiensis* and *V. picta*, are now known from northwestern Panamá and *V. capitata* has been collected as far southeast as Cerro Jefe. Judged by the available data those collections were made at elevations and in life zones similar to those in which the species occur in Costa Rica.

Morphology

HABIT. The thecophylloid vrieseas are primarily epiphytic, although many species will grow terrestrially. The majority of species are acaulescent with leaves densely rosulate but, with a few species becoming extemely long caulescent. There apparently are taxonomic as well as ecological correlations associated with caulescence. *Vriesea williamsii* and a few related species, the only thecophylloids that regularly exhibit extreme caulescence, have stems ranging from ca 6 cm to over 1 m long. Extreme caulescence is frequently encountered in terrestrial individuals.

VESTITURE. The single most characteristic feature of the Bromeliaceae is the almost universal presence of absorbing trichomes on leaf surfaces. These structures are wanting in only *Navia lopezii* L.B. Smith, where their absence apparently is a derived condition resulting from the failure of initial cells to subdivide (Robinson, 1969).

The general structure of the tillandsioid trichome has been described by Tomlinson (1969) and Benzing (1976) and illustrated with great clarity by Ehler (1977). The lower portion of the trichome consists of three cell types, 1) two or more small basal foot cells, 2) two to three stalk cells and 3) a large distal dome cell. This stem-like structure supports a shield one cell layer thick that consists of four central cells, immediately distal to the dome cell and peripheral concentric series of ring cells. Each series contains twice as many cells as the adjacent inner ring cell series. The of the outermost series, or wing, frequently are elongate and distinct in appearance from the subtending ring cells. The wing cell series usually contains more than twice the number of cells in the preceding ring cell series and the cells often are allomorphic, producing asymmetric, or in extreme cases, "tailed" shields. Unlike shield cells, which are dead at maturity, cells of the stalk are living. The distal dome cell has a dense protoplast, an enlarged nucleus, an elaborated plasmalemma and numerous mitochondria, modifications that Dolzmann (1964) believed to be involved with the absorptive function of these trichomes. In addition the trichomes have a specialized pattern of cutinization which serves to direct water and solutes to the dome cell and ultimately to the leaf interior (Ehler, 1977). Moreover, this cuticular pattern coupled with the hygroscopic changes in orientation of the shield cells enables the trichomes to function as "one-way valves" in water and solute uptake. This mechanism was reviewed by Benzing (1976).

Within the family, the structure of these absorbing trichomes is variable. An increase in complexity is apparently linked to adaptive radiation into the epiphytic habitat. Moreover, this increase in complexity has apparently occurred along two separate lines. Such a view is supported by the fact that scale structure of epiphytic taxa in the Bromelioideae is strikingly different from the structure of scales found in the Tillandsioideae (Tomlinson, 1969; Benzing, 1976). The scales of the former subfamily, like those of the Tillandsioideae, have a well developed shield, but they lack the highly organized arrangement of central disc and peripheral ring cells found in the latter subfamily (Fig. 2).

Variability in wing structure is frequently encountered within the blade of a single leaf

or bract. The shields in the central portion of the leaf are more or less symmetrical but near the leaf margin the shield becomes progressively more asymmetrical. Moreover, scales of the adaxial and abaxial surfaces are frequently differentiated from each other by size and/or density, and in the extreme case of *Vriesea capitata*, the trichomes from opposing leaf surface display radically different wing morphologies (Figs. 3 & 4). The most striking examples of variation in trichome morphology in the thecophylloid vrieseas are found between trichomes from sheath and blade areas of the same leaf (cf. Figs. 3, 4, 5, 7, 8, 9, 10). The sheath area trichomes from different species tend to be similar morphologically (Figs. 5, 7, 8). This similarity becomes even more striking when one considers that the blade trichomes of the same species show distinct differences (Figs. 3, 4, 9, & 10). Interspecific similarity in sheath trichomes and frequent dissimilarity between those from blade regions may be due to convergence in function and structure. Since these taxa are tank epiphytes, the area of greatest water and nutrient availability is within the tightly overlapping leaf sheaths thus trichomes of the sheath area will play a potentially important role in absorption. Involvement in this essential process may have limited the toleration for variability in structure and resulted in the maintenance of similar trichomes in divergent taxa.

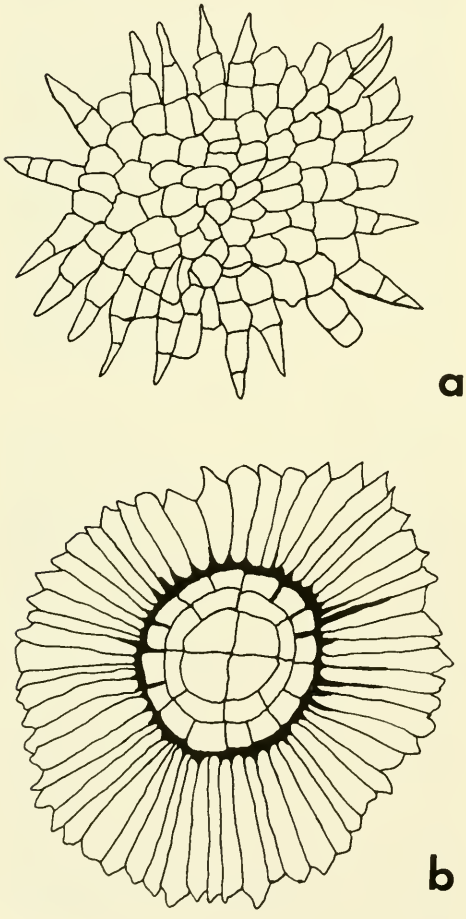
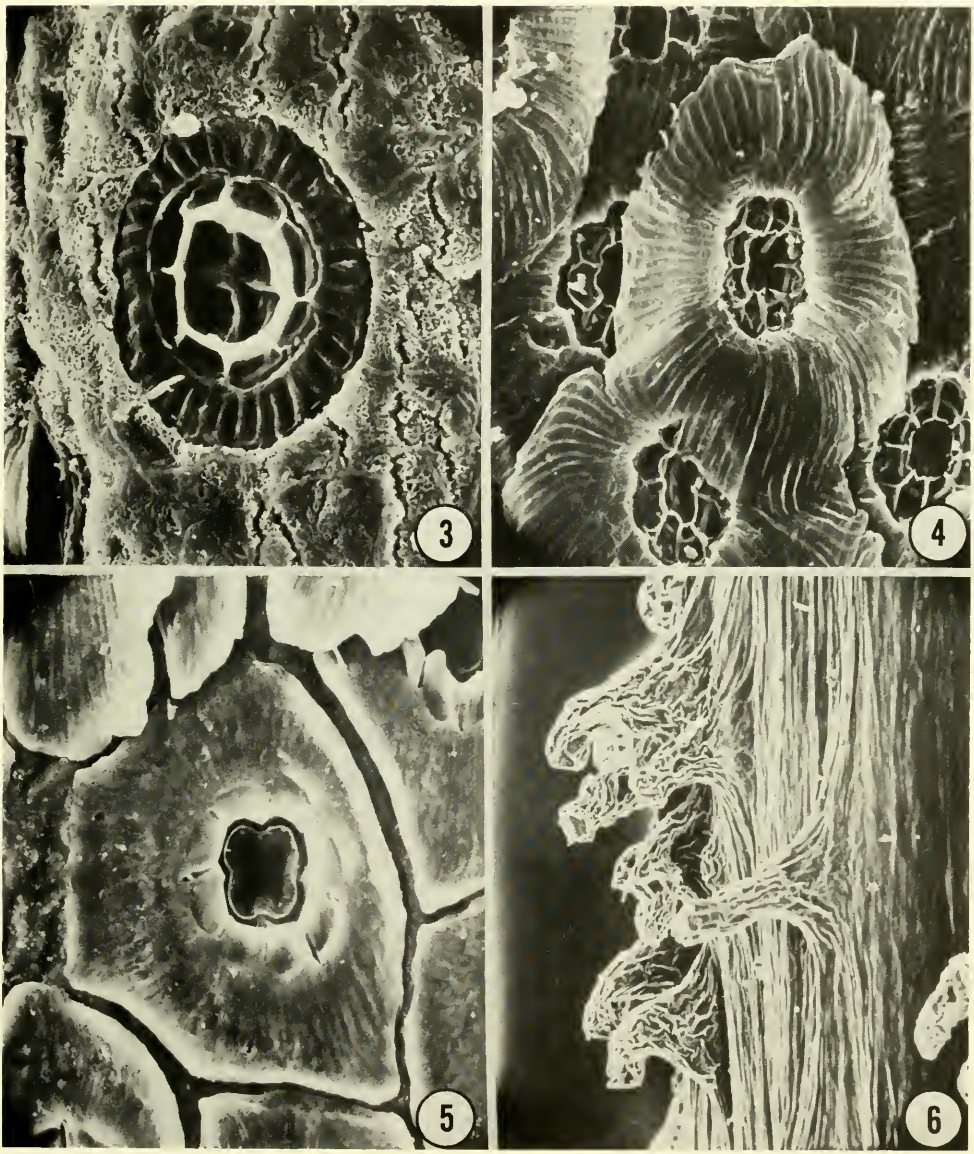


Fig. 2. Arrangement of cells in the shield of absorptive trichomes; a) Pitcairioideae and Bromelioideae, and b) Tillandsioideae.

The taxa surveyed in this study have a common shield morphology of four central cells and one series of eight ring cells; however, the number of wing cells can be either 16 or 32. As already mentioned, great variation in trichome morphology is encountered between the sheath and blade area of the same leaf, as well as between the abaxial and adaxial blade surfaces. This emphasizes the need to utilize trichomes from homologous areas in any comparative study.

In addition to the ubiquitous foliar trichomes, the species under consideration also display other epidermal ornamentation, which is diagnostic of some taxa. The axis of the scape and inflorescence of *Vriesea triflora* is covered with densely packed papillae of characteristic appearance (Fig. 6). The rachis and scape of *V. diffusa*, a closely related species, also have these papillae, although they are not as well developed. While no other thecophylloids have these structures, the floral bracts of many commonly have small wart-like excrescences, as well as pellucid, castaneous margined, punc-



Figs. 3-6. 3. Foliar trichome from the abaxial leaf-blade surface of *Vriesea capitata*, X ca. 375 *(Utley & Utley 4477)*. 4. Foliar trichome from the adaxial leaf-blade surface of *Vriesea capitata*, X ca. 190 *(Utley & Utley 4477)*. 5. Foliar trichome from the leaf-sheath area of *Vriesea triflora*, X ca. 300 *(Utley & Utley 4477)*. 6. Papillae on the inflorescence of *Vriesea triflora*, X ca. 85 *(Utley & Utley 5193)*.

tulae and minute pits; the punctulae apparently represent poorly developed or abortive stomata and the pits are associated with absorptive trichomes.

LEAVES. The leaves of thecophylloid vrieseas are typically densely rosulate on a much shortened stem or occasionally spirally arranged on an elongated caudex. The caulescent taxa rarely retain leaves over the entire length of the stem; the older regions are usually denuded or covered with the remains of leaf bases, while functional leaves are found at the distal portion of the stem. The leaves consist of two morphological regions, the sheath and blade areas, which can usually be delimited fairly accurately, but occasionally the zones merge so gradually that they can only be approximately defined.

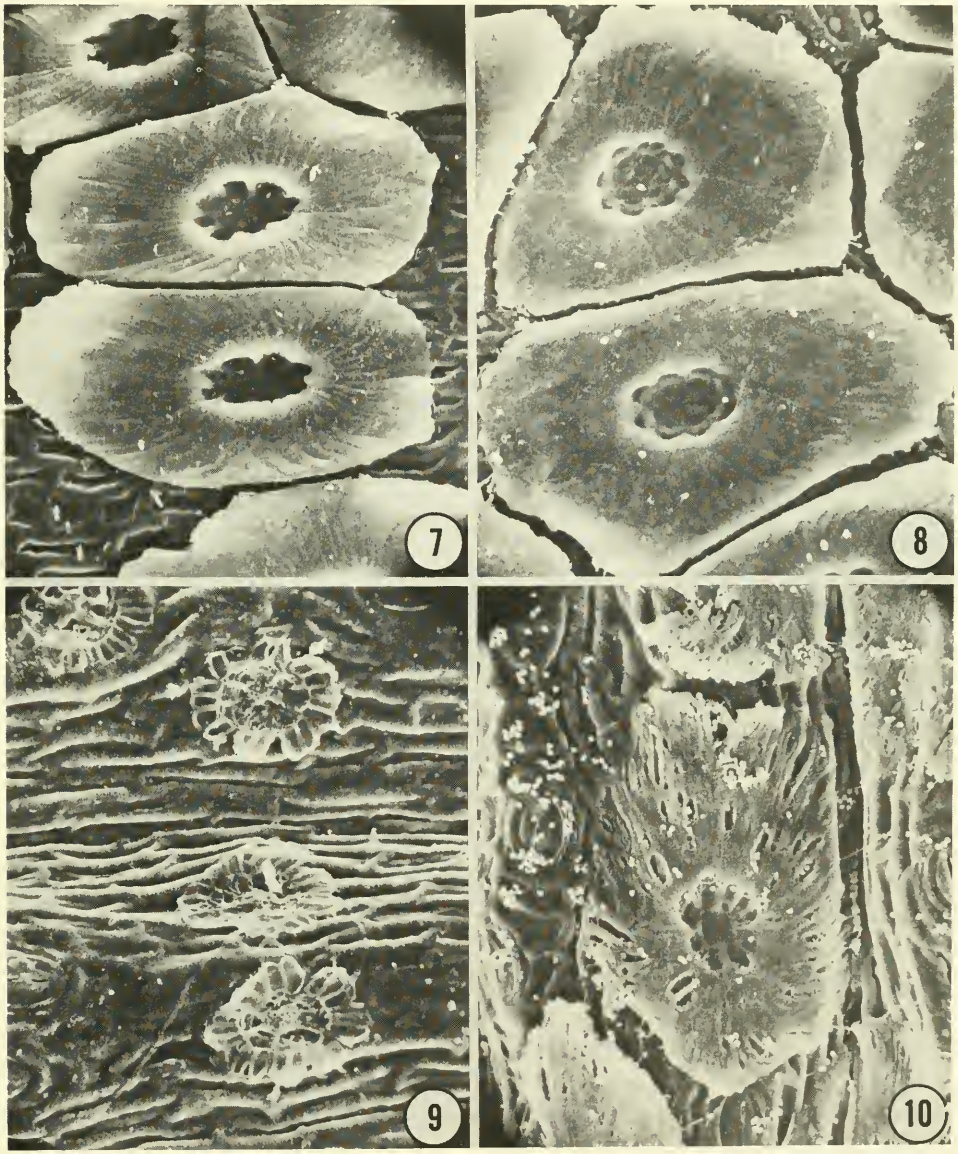
The sheath comprises that portion of the leaf delimited by the bounds of an open "S" curve; in addition there are frequently characteristic trichome morphologies and color or marking patterns, which change at or near the sheath-blade interface. As previously mentioned, the trichomes in the sheath area tend to be more highly developed and are very densely packed, frequently forming a mosaic pattern of shields. The abaxial surface or occasionally both surfaces may be densely castaneous, and in the distal portion of the sheaths, the foliar markings characteristic of many thecophylloids become evident. The leaf blade is that portion of the leaf distal to the sheath. Shapes encountered range from ligulate to elongate-triangular, the entire range of shapes occasionally being found within the rosette of a single individual. The blades are frequently suffused with various shades of red, or maroon, a condition most evident when a plant is about to produce an inflorescence. However, plants in exposed locations are frequently colored throughout the year. In addition to general suffusion, many thecophylloids have wavy transverse lines or straight longitudinal stripes of pink, red,purple or maroon. The wavy transverse bands are frequently discernible in totally green leaves as wavy darker green lines.

Leaves of taxa under consideration were sectioned and mounted using the techniques of Robinson (1969). The following generalized description of leaf structure is based on these slides.

The cells of the adaxial epidermis, which frequently contain spherical, spinulose silica bodies, are comparatively flat in crosssection and the anticlinal walls are thickened and sinuous. The hypodermis is differentiated into an outer sclerotic layer with thickened walls and an inner layer of thinner walled "water storage" cells with anticlinally extended, frequently plicate, walls. Immediately beneath the hypodermis is the chlorenchyma, which consists of two cell forms: 1) a compact area of isodiametric or slightly elongate cells which are most abundant over the intercostal aerating canals, extending down the sides of the vascular bundles or up the adaxial bundle buttresses and at times completely overtopping the vascular bundles, and 2) stellately branched cells which occur as a ramifying network within the aerating canals. The vascular bundles are located within strongly sclerified bundle sheaths, which form "figure-8's" around the vascular elements of the principal veins. While the central bar of the "8" is variable in degree of development it often is prominent. The adaxial surfaces of the bundle sheaths are typically strongly buttressed, with the distal portion of the longer buttresses coming within one cell layer of the sclerotic hypodermis; the abaxial surface is rarely buttressed to the same degree. Below the vascular bundles is the abaxial "water storage" hypodermis which frequently extends to the vascular bundles and also beneath the aerating canals where it is interrupted by the substomatal chambers. Beneath the abaxial water storage hypodermis is an outer layer of

sclerotic cells with very much thickened anticlinal and internal periclinal walls.

There are taxa that are sufficiently unique in one or more anatomical features to be recognized on the basis of their leaf anatomy alone (e.g. *V. bracteosa* and *V. capitata*), however the sample size involved in this survey is not adequate to support any broad generalizations regarding the use of anatomical characters in the classification of the



Figs. 7-10. Foliar trichomes of vrieseas. 7. From leaf-sheath area of *Vriesea triflora*, X ca. 275 *(Utley & Utley 5193).* 8. From the leaf-sheath area of *Vriesea diffusa*, X ca. 275 *(Utley & Utley 1857 c).* 9. From the abaxial leaf-blade surface of *Vriesea triflora, X ca. 275 (Utley & Utley 5193)* 10. From the abaxial leaf-blade surface of *Vriesea diffusa*, X ca. 275 *(Utley & Utley 1857 c).*

thecophylloid vrieseas. There is apparent variation in the amount of hypodermis, the amount and arrangement of sclerenchyma and the arrangement of chlorenchyma, indicating that further study of leaf anatomy is warranted.

INFLORESCENCES. The basic thecophylloid vriesea inflorescence consists of a scape supporting a once-compound inflorescence varying in length from one or a few centimeters (subcapitate) to several decimeters. The scape is usually erect but is occasionally curved laterally or even pendent. It is provided with a series of spirally arranged scape bracts which are transitional in form between leaves and the primary bracts of the inflorescence. The bracts consist of a sheath and blade area, which, as in the case of leaves, are occasionally difficult to delimit precisely. The length of these bracts relative to the internodes, and their color and marking, frequently are of use in identifying species. The primary bracts, which subtend the lateral branches, are similar in shape and morphology to the upper scape bracts, but they are often more intensely colored and are usually spreading or even recurved in contrast to the erect posture of the scape bracts. A third series of bracts, the floral bracts, subtends the flowers. The morphology of these bracts has been used to separate species or species groups.

The condensation of lateral branches and concomitant enlargment of primary bracts influenced André (1889) to establish *Thecophyllum* and, although the genus is no longer recognized, this basic inflorescence structure is fairly distinctive within *Vriesea*. The inflorescence consists of a panicle in which the secondary branch system has become reduced to the point that the lateral branches are sessile or short pedunculate in the axils of enlarged primary bracts. The flowers are alternately or suboppositely spicate, racemose on a short axis, collateral or subfasciculate. The simplest of the inflorescences encountered is the single flowered spike of *Vriesea singuliflora*, where the compound nature of the inflorescence is revealed only by the presence of a floral bract and a primary bract subtending each flower. In contrast the well-developed lateral spikes or racemes of *V. greenbergii* contain three to five flowers (Fig. 19). In several species, including *V. ororiensis*, the lateral fascicles regularily contain two flowers, with variation largely confined to differences in peduncle and pedicel length (Fig. 11).

The general morphological trends exhibited by the thecophylloid vrieseas are condensation or abortion of the peduncles, pedicels or floral rachises and a reduction in the number of flowers per lateral branch. The diversity of inflorescence forms displayed by this group can be derived through a reduction series from the laxly flowered panicle commonly encountered in *Vriesea*.

CALYX. The calyx is imbricate in bud and closes around the developing capsule after anthesis. Because the sepals are often thickly coriaceous, the calyx-envelope potentially serves as a barrier against predation in early stages of fruit development. The durability of the sepals has resulted in these structures being utilized extensively in traditional species delimitation. The size, shape and texture

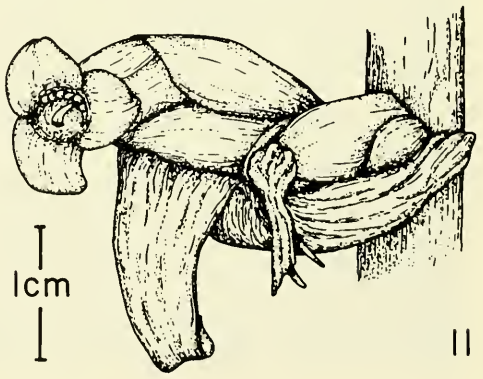


Fig. 11. Lateral inflorescence branch and flowers of *Vriesea ororiensis* showing the two colateral flowers and the subtending primary bract.

of the sepals are useful but the general range in the former two characters and the qualitative nature of the latter make an "a posteriori " application imperative.

COROLLA. The three free petals of the corolla are imbricate in bud, inserted alternately to the sepals and bear two scale-like appendages near the base. At anthesis the corolla may assume a wide variety of shapes ranging from campanulate to more or less tubular to strongly zygomorphic (cf. Figs. 11-14). The petals vary in size from about one cm to over five cm in length and from translucent white or greenish-white to chartreuse or yellow-green. The corollas of this group of vrieseas are highly variable; many species that are very similar or almost identical vegetatively or in fruit, have vastly differing floral structures and phenologies.

ANDROECIUM. The androecium is characteristically asymmetric. The filaments are displaced so that the anthers, which are usually connivent by their lateral margins, form a hood over the gynoecium (Fig. 12). Occasionally the androecial hood is represented by two pairs of three anthers, or rarely the anthers are free but the filaments are displaced so that the anthers are dorsal to the stigma.

GYNOECIUM. The ovary is inserted on the receptacle in such a way that the petal appendages contact the gynoecium at the base of the style, loosely partitioning the intrafloral chamber into two compartments. The style is usually bent in a dorsal direction at the style-ovary junction and then arches distally until, near the stigma, it curves ventrally, orienting the stigma surface away form the overarching androecial hood. The degree of proximal torsion varies from almost a right angle to practically none and the ventral torsion of the stigmatic surface varies but is usually present to some degree (Figs. 12 & 13).

As previously mentioned the thecophylloids share a unique stigmatic structure with a few other species in section *Xiphion*. The stigma presents the appearance of three circular cups deposited symmetrically around a common axis (Fig. 15c). The remainder of the vrieseas have stigmas that are somewhat flattened and expanded distally. Deriving the thecophylloid stigma from the latter form through progressive flattening, expan sion and inrolling of the lateral margins, followed by, or concomitant with, an axial torsion of the tubular stigma branches is not conceptually difficult. The distribution of this stigmatic type and its consequent significance in classification is not entirely known; the results of a preliminary survey and some tentative conclusions are presented in the section dealing with intergeneric relationships.

FRUIT. The fruit is a tough, septicidal capsule, which varies in shape from fusiform to strongly obovate, castaneous to olive-green in color and from about 1.5-5.5 cm long. At maturity the fruit splits basipetally and the chartaceous septa break down or tear free from the outer wall releasing the plumose appendaged seeds, which are wind dispersed.

SEED. The seeds, which are fairly uniform within and among the species, have a plumose appendage derived from the integuments. The outer integument splits longitud-

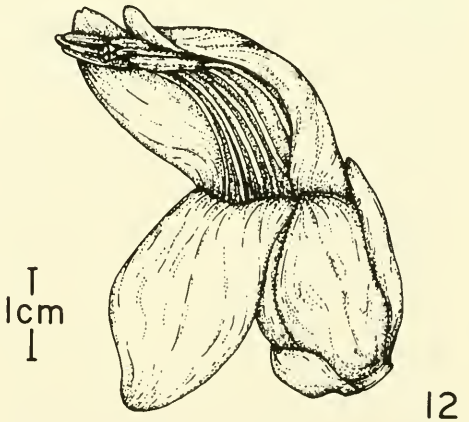


Fig. 12. Flower of *Vriesea nephrolepis*.

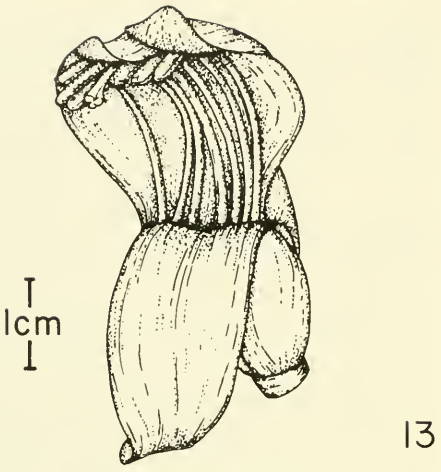


Fig. 13. Flower of *Vriesea williamsii.*

inally into hair-like segments that are attached only at the proximal end of the seed, thus forming a parachute-like coma. The inner integument also becomes longitudinally divided, but remains attached along the length of the seed coat. Seed characteristics have not yet proven of value within the thecophylloids. The development and taxonomic significance of seeds in Bromeliaceae is reviewed by Downs (1974) and Szidat (1922).

REPRODUCTIVE BIOLOGY

The reproductive biology of the Bromeliaceae has not been studied to any great extent. McWilliams (1974) presented a survey of recent work and a list of putative breeding systems for 14 taxa. Brewbaker and Gorrez (1967) elucidated the genetics of self-incompatibility in the cultivated pineapple. The state of our knowledge concerning pollen vectors is only slightly better. There have been reports of bat, hummingbird, bee, fly and wind pollination (McWilliams, 1974). With respect to the thecophylloid vriesea species there are only two reports. Porsch (1932) considered *Thecophyllum* to be bat pollinated and Salas (1973) inferred bat visitations to a species that he identified as *Thecophyllum irazuense.*

The thecophylloid vrieseas present a variety of phenologies: 1) day-blooming taxa, 2) crepuscular taxa, and 3) night-blooming taxa. The day-blooming taxa have greenish or greenish-yellow flowers and the primary bracts are usually red to pink, occasionally maroon or rarely brown at anthesis. Members of this group can be further subdivided based on the orientation of the inflorescence at anthesis. In *V. ororiensis* the inflorescence is erect and in *V. leucophylla, V. hainesiorum* and *V. uxoris* inflorescence posture is downwardly slanting to strongly pendent. This entire group may be hummingbird pollinated and I have made field observations for most of the species. In the case of *V. ororiensis* extensive observations and photographs are available. *Vriesea ororiensis* usually occurs in large local populations and flowers during the dry season. The exact time of flowering varies among populations, but within a population flowering is synchronous. Within an inflorescence flowering is sequential, beginning basally and continuing acropetally, with a few flowers at a time (one to four) opening over a period of several days to more than a week. The petals begin to expand prior to sunrise, sometimes as early as the preceding evening, and about dawn the corolla has assumed the form of a

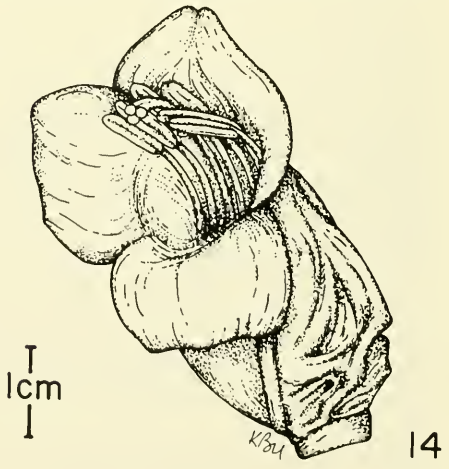


Fig. 14. Flower of *Vriesea hygrometrica.*

narrow tube, with a distal portion of each petal flaring slightly. The androecial hood, which has been in tubular configuration around the style and stigma, separates ventrally and assumes a dorsal hood configuration over the ventrally facing stigma (Fig. 11). Pollen is shed in clingy masses about dawn or shortly thereafter. Stigma receptivity, as measured by the production of viscid drops, occurs concomitantly with pollen release or as much as an hour later. The flowers last a single day and have usually become flaccid by the second morning, or on rare occasions they persist through the second day but become senescent by the third morning. Hummingbirds begin to work the opening flowers before sunrise and continue through late afternoon; they hover or occasionally rest lightly on a lower primary bract while visiting the open flowers and then depart to visit other inflorescences in the vicinity (Fig. 16). Because of the paucity of open flowers on an inflorescence, self pollination is kept to a minimum and the generally high density of individual plants increases pollinator fidelity and concomitantly outcrossing (Baker, 1961). *Vriesea leucophylla* is also visited by hummingbirds, and although extensive observations are not available the phenology and population density are similar to *V. ororiensis* and the same generalizations may hold true. *Vriesea hainesiorum* is similar to *V. leucophylla* but the former species is consistently smaller and has fewer flowers per inflorescence. Although no potential pollinators have been observed visiting *V. hainesiorum*, the general form of the inflorescence, with red scape bracts and primary bracts and diurnal flowers, argues for ornithophilous pollination. *Vriesea uxoris* also possesses a syndrome of characters that suggest hummingbird pollination. Hummingbirds have been observed hovering near the species but no actual visitations have been recorded.

Only two taxa, *V. balanophora* and *V. viridis*, are known to be crepuscular. Both species have white flowers and maroon sepals, whereas the primary bracts are green with prominent wavy maroon transverse bands or occasionally entirely maroon in *V. viridis*. This syndrome agrees with that proposed by Baker (1961) for plants adapted to crepuscular, ornithohilous pollination. Phenological observations are available only for *V. viridis*. Anthesis begins in the early afternoon and is completed by about 5:00 p.m. As in *V. ororiensis* the direction of flower maturation is acropetal and only a few flowers are open on any given day; moreover, this taxon also tends to occur in extensive local populations. On the two occasions observations were made, hummingbirds visited the flowers from about 3:00 p.m. until light was insufficient for further observations; even at this point, flight noise was audible in the vicinity of the plants. Other crepscular vectors possibly visit this taxon, however the flowers are odorless and hummingbirds work the inflorescences diligently, indicating that the

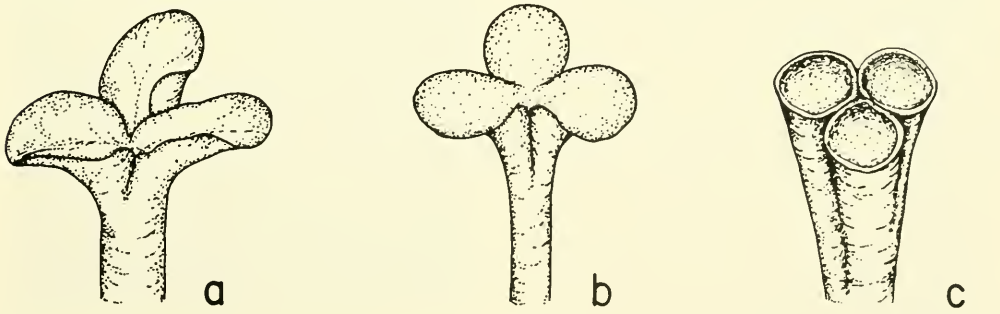


Fig. 15. Diagrammatic representation of stigma forms.

flowers are probably primarily ornithophilous.

In contrast to the diurnal and crepuscular taxa which seem to be groups of more or less similar species, the nocturnal taxa are subdivisible into two distinct groups based on inflorescence structure. The first of these groups consists of species with capitate to elongate inflorescences, with collaterally biflowered lateral branches and flowers sessile or subsessile in the axils of the primary bracts. Corolla shape varies from open cylindric in *V. stenophylla* to strongly zygomorphic in *V. williamsii* and *V. nephrolepis*. In the latter case two of the petals are frequently associated into a dorsal hood and the third petal is positioned as a ventral, labellum-like structure (Fig. 12 & 14).

Based on observations of living flowers, Porsch (1932) suggested the possibility of bat pollination in an unidentified species of night-blooming Costa Rican *Thecophyllum*; he likely observed a member of this group. Salas (1973) studied a species of the paniculate subgrouping with strongly zygomorphic flowers. The determination of the species as *Thecophyllum irazuense* was in error however, because this name is a synonym of the day-flowering, ornithophilous *Vriesea ororiensis*. Unfortunately, voucher specimens were not deposited, but the extensive floral description and the site location provided by Salas leave little doubt that the taxon he studied was *Vriesea nephrolepis (Thecophyllum werckleanum)*. Salas observed bats flying among the flowering plants from 6:30 p.m. until 11:00 p.m. and inferred bat visitations to the bromeliad flowers by trapping the animals and examining fur for presence and type of pollen. He reported finding copious amounts of *"Thecophyllum"* pollen on the tops of the bats' heads and the sides of their faces. He also noted that the flowers began to open about 5:00 p.m. and had a musky odor. My observations of this species generally bear out Salas' reports on the time of anthesis and smell of the flowers, however many flowers in the population I observed began opening as early as 3:30 p.m. and several were fully open by 5:00 p.m. In addition, hummingbirds were photographed visiting open flowers in a manner which was as conducive to pollination as visitations by bats.

The second major group of nocturnal taxa consists of species with well developed lateral branches with obvious peduncles, pedicels or rachises and frequently more than two flowers per branch. Corolla shape varies from campanulate in *V. pedicellata* to strongly zygomorphic in *V. umbrosa*.

Phillip DeVries (pers. comm.) has observed bats visiting what is probably *V. latissima* in the Monte Verde forest perserve in Costa Rica. I have observed that *V. umbrosa* has a decidedly sweet, spicy odor during the early evening. This odor, in conjunction with nocturnal anthesis, argues strongly for pollination by a night flying insect but confirmatory observations are lacking.

In summary, the thecophylloid vrieseas present a wide range of floral and inflorescence types as well as divergent phenologies. A variety of potential pollinators has been observed or inferred on the basis of presumptive evidence.

INTRAGENERIC RELATIONSHIPS

The genus *Vriesea* is distinguished from the remainder of the Tillandsioideae on the basis of distichous inflorescences and free appendaged petals. It is subdivided into two subgenera and two sections on the basis of seed and floral characters. The subgenus *Alcantarea* is characterized by seeds that have the apical appendage enlarged and divided to form a short coma in addition to the usual basal coma and ephemeral petals that become flaccid soon after anthesis. In contrast, subgenus *Vriesea* has a single basal plumose appendage and comparatively durable petals.

The subgenus *Alcantarea* contains only seven species and has not been further subdi-

vided. Subgenus *Vriesea*, however, has over 200 species and contains two sections which are separated from each other on the basis of androecial structure. In section *Vriesea* the stamens are exserted from the corolla, whereas in *Xiphion* they are included. This division is correlated with several other characters. Section *Vriesea* contains species that frequently have highly colored bracts which are red, yellow or orange, but section *Xiphion* contains species that generally have dull, green or brown colored bracts. Furthermore, section *Vriesea* has a center of diversity in southeastern Brazil whereas *Xiphion* has a center of diversity in northern South America and southern Central America, with a secondary center of diversity in southeastern Brazil.

Within section *Xiphion* the thecophylloids are most closely allied to a complex of low to middle elevation, secund-flowered species which are concentrated in Costa Rica, Panamá and Brazil. However, a few species are distributed through northern Central America, the Antilles and northern South America (Smith, 1941). Most species of this group exhibit the three-cupped stigmatic structure typical of the thecophylloids (Fig. 15c). The only taxa examined that lacked this stigmatic structure were *V. gigantea* Gaud. and *V. unilateralis* (Baker) Mez from southern Brazil. Both of these species have a stigma form consisting of three flattened, suborbicular branches (Fig. 15b). Moreover, the secund-flowered vrieseas have nocturnal flowers which are essentially identical to the larger, campanulate, nocturnal flowers of the thecophylloids.

Fig. 16. Hummingbird *(Panterpe insignis)* visiting *Vriesea ororiensis.*

More data are needed but the similarity in floral morphology, including the unique stigmatic structure, tempt one to hypothesize that the thecophylloid vrieseas and (at least the majority of) the secund-flowered species of section *Xiphion* share a common origin.

If the foregoing assumption is true then the ancestral group of the thecophylloids likely had night-blooming flowers. This is suggested by the predominance of night-flowering in the thecophylloids and their secund-flowered allies. If this is so, and if one accepts the likelihood that the montane species endemic to Costa Rica envolved *in situ*, then it follows that the ornithophilous taxa have undergone adaptation to avian pollination independently of other ornithophilous vrieseas. Even more interesting is the corollary that these diurnal, ornithophilous species are derived from a nocturnal, potentially chiropterophilous, ancestor, a situation that is the converse of the usual evolutionary sequence (Grant and Grant, 1968; Skog, 1976).

The thecophylloid vriesea species can be divided into three basic groups on the basis of inflorescence morphology. The first of these groups, the pedicellata complex, is characterized by well-developed secondary inflorescence branches with obvious peduncles, pedicels, or rachises and usually more than two flowers per lateral branch. The other groups, ororiensis and hygrometrica

complexes, are characterized by collaterally biflowered lateral inflorescence branches with little, if any, peduncle, rachis or pedicel development.

Four species groups can be recognized within the pedicellata complex on the basis of pedicle length, the size and texture of floral bracts and floral morphology. The first of these, the pedicellata species group, is characterized by membranous floral bracts which are shorter than or equal to the pedicels, and campanulate flowers. The pedicellata species group is similar to the triflora group that is distinguished by subcoriaceous to coriaceous floral bracts, which exceed the pedicels, and by the papillose surfaces of the inflorescences. As in the pedicellata group, the flowers are campanulate. The third species group, the umbrosa group, is distinguished by coriaceous floral bracts which exceed the pedicels, by the smooth surfaces of the inflorescences and by the bilaterally symmetrical corollas. The fourth species group in the pedicellata complex, the latissima species group, contains a single species, *V. latissima*. This species is most similar to the species in the umbrosa group, but is distinguished by its larger floral bracts and flowers and much stouter inflorescence branches.

In the second of the complexes, the ororiensis complex, the floral bracts are shorter than or about equal to the sepals and the inflorescence usually is elongate. This complex contains five species groups that are differentiated on the basis of floral bract length, inflorescence orientation, phenology and growth habit. The first of these groups, the ororiensis species group, is characterized by diurnal or nocturnal anthesis, floral bracts that are no more than one half as long as the sepals, and erect inflorescences. This group consists of three taxa which are very similar in the vegetative and fruiting states. However, they are readily separable in flower on the basis of phenology, primary bract color and floral morphology. Members of this group display floral syndromes typical of adaptation to bat or hummingbird pollen vectors. The second group, the balanophora group, is characterized by floral bracts that are about as long as the sepals, crepuscular anthesis, maroon or purple sepals and cinerous pubescence on the abaxial leaf surfaces. This group is most similar to the leucophylla species group which is characterized by pendent inflorescences, diurnal anthesis and floral bracts that are about as long as the sepals. The species in this latter group are apparently adapted for diurnal hummingbird pollination. The fourth group consists of a single species, *V. uxoris*, which has a pendent inflorescence and diurnal flowers. This species differs in floral morphology, ecology and trichome type from the pendent-inflorescenced species in the leucophylla group and is best considered as distinct from these species. The final group in this complex, the stenophylla species group, consists of species with nocturnal anthesis, strongly zygomorphic corollas, a caulescent habit and tank-roots. Diurnal anthesis in conjunction with other characteristics typical of ornithophily (Faegri and van de Pijl, 1971) is found only in the ororiensis complex. Significantly this complex contains those species that have been the most successful in adapting to the montane environment. Moreover, the presence of crepuscular anthesis and nocturnal anthesis in conjunction with a chiropterophilous syndrome (Faegri and van de Pijl, 1971) indicates that this complex is potentially adapted to a diversity of pollinators. Neither the pedicellata complex nor the hygrometrica complex exhibits a similar pollinator diversity and these groups are poorly represented at higher elevations (i.e. above 2,000 m). Perhaps the pollinator diversity of the ororiensis complex has contributed to their success in the higher montane regions.

The third complex, the hygrometrica complex, contains taxa with floral bracts that are usually much longer than the sepals and inflorescences, which are frequently subcap-

itate or short, dense cylindric. This complex consists of three species groups. Two of these, the comata group and the hygrometrica group, are closely allied and are distinguished from each other on the basis of leaf size and markings, density of the inflorescence and primary bract color. The comata group contains *V. comata* and *V. attenuata*. The latter species has floral bracts that are regularly shorter than or equal to the sepals. The two taxa are virtually indistinguishable in the vegetative state but fertile material is readily indentifiable. In light of its overall similarity to *V. comata, V. attenuata* is best considered part of this complex despite the aberrant floral bract length. I also place *V. singuliflora* in the comata group. The floral bracts of this species are also shorter than the sepals. However, its castaneous leaf sheaths, unmarked green leaves, apparently white, nocturnal flowers and occurrence at relatively low elevations (300 m), suggest a relationship with the comata group. In contrast to the usually green leaves of the comata species group, the leaves of the hygrometrica group are frequently suffused with purple to maroon and often have longitudinal or transverse lines of red, purple or maroon. Moreover, the inflorescences of this group elongate post anthesis, a condition which is not encountered in the comata species group. The third group in the complex, the bracteosa species group, is characterized by its dense, capitate inflorescences, green unmarked leaves in an ascending rosette and by the presence of a well developed layer of extrafascicular sclerenchyma in the adaxial hypodermis.

The arrangement of the Middle American thecophylloid vrieseas into species groups is summarized below (Table 1).

In summary, the thecophylloid vrieseas may be closely allied to a group of secund-flowered species in section *Xiphion*. This alliance is supported by floral morphology, phenology and a common stigma structure. The thecophylloids are divisible into groupings on the basis of the structure of the lateral

TABLE 1. Species groups of Middle American thecophylloid vrieseas.

I. PEDICELLATA COMPLEX	
A. Pedicellata group	*V. leptopoda & V. pedicellata*
B. Triflora group	*V. diffusa & V. triflora*
C. Umbrosa group	*V. greenbergii & V. umbrosa*
D. Latissima group	*V. latissima*
II. ORORIENSIS COMPLEX	
E. Ororiensis group	*V. lyman-smithii, V. nephrolepis & V. ororiensis*
F. Balanophora group	*V. balanophora, V. luis-gomezii & V. viridis*
G. Leucophylla group	*V. hainesiorum, V. leucophylla & V. vietoris*
H. Uxoris group	*V. uxoris*
I. Stenophylla group	*V. picta, V. stenophylla & V. williamsii*
III. HYGROMETRICA COMPLEX	
J. Comata group	*V. attenuata, V. comata & V. singuliflora*
K. Hygrometrica group	*V. hygrometrica, V. kathyae & V. notata*
L. Bracteosa group	*V. bracteosa & V. capitata*

inflorescence branches, inflorescence form and the relative length of floral bracts and sepals. In contrast to the general pattern of nocturnal anthesis found in *Xiphion*, several thecophylloids have developed diurnal anthesis coupled with an ornithophilous floral syndrome in addition to creuscular anthesis in conjunction with a syndrome adapted to pollination by a crepuscular vector. Moreover, this variety of pollination syndromes is confined to a single group of species that have been highly successful in the middle and upper montane environments. The success of these species at higher elevations likely is related to their adaptation to a variety of potential pollinators.

TAXONOMIC TREATMENT

Although the thecophylloid vrieseas have not been given nomenclaturally valid status as a group within section *Xiphion*, they and their allies form a distinct, probably phyletically related alliance. However, further knowledge of the group and the remainder of *Xiphion* is an essential prerequisite to the erection of a formal intrasectional framework.

The thecophylloids and their allies can be easily separated from the remainder of the Costa Rican vrieseas by their unique three-cupped stigmatic surfaces. Those species that were or would have been considered in the genus *Thecophyllum* by Mez (1934-1935) can generally be separated from their secund-flowered allies on the basis of general inflorescence structure combined with development and form of the lateral inflorescence branches and primary bracts. The following synoptic key summarizes the salient differences between the thecophylloid vrieseas and their allies.

1. Inflorescences simple or compound; the lateral branches much exceeding the primary bracts, the floral bracts exceeding the sepals and the peduncles and rachises smooth, definitely not papillose .... thecophylloid allies

1. Inflorescences compound, or if appearing simple than a series of two bracts subtending each flower indicates a compound inflorescence; primary bracts exceeding or about equaling the lateral branches; if the lateral branches exceed the primary bracts then the floral bracts are shorter than the sepals or the rachis and peduncles are densely papillose .... thecophylloid vrieseas

The characters that are used to separate the species of thecophylloids have already been detailed, but a brief discussion of the measurement of floral parts is necessary before the following key to species can be used effectively. Floral parts especially the floral bracts, sepals and petals, shrink on drying, in some cases resulting in as much as 25% change in dimensions. Therefore floral material used in identifying species must be fresh, liquid preserved or rehydrated by boiling the flowers. With the exception of floral parts the following key is based on dried material.

ARTIFICIAL KEY TO THE SPECIES OF MIDDLE AMERICAN THECOPHYLLOID VRIESEAS

1. Proximal lateral branches 1-flowered

    2. Floral bracts longer than wide or the two dimensions about equal; sepals to 1.2 cm long.

        3. Floral bracts as long as or shorter than the pedicels ..... *V. pedicellata*

        3. Floral bracts longer than the pedicel ..... *V. diffusa*

2. Floral bracts wider than long, subrotund; sepals 1.5 cm long .... *V. singuliflora*

1. Proximal lateral branches bearing 2 or more flowers.

4. Lateral branches of the inflorescence highly developed, frequently more than 2-flowered; peduncles, rachises or pedicels elongated, usually slender.

5. Floral bracts membranaceous, shorter than or about equalling the pedicels.

6. Lateral branches 5- to 8-flowered; floral bracts 1.4-1.8 cm long; sepals 1.4-1.6 cm long; petals 2.5-2.7 cm long ..... *V. leptopoda*

6. Lateral branches 2- to 5(6)-flowered; floral bracts 0.4-0.8 cm long; sepals 0.8-1.2 cm long; petals 1.8-2.1 (2.4) cm long. ..... *V. pedicellata*

5. Floral bracts chartaceous to subcoriaceous, distinctly exceeding the pedicels.

7. Rachis of the inflorescence, peduncles or pedicels densely papillose.

8. Floral bracts 0.9-1.2 cm long; petals 1.9-2.0 cm long; leaf blades with wavy transverse lines proximally ..... *V. triflora*

8. Floral bracts 0.5-0.7 cm long; petals 1.5-1.6 cm long and leaf blades with longitudinal purplish lines proximally ..... *V. diffusa*

7. Rachis of the inflorescence, peduncles and pedicels glabrous or with punctulae, definitely not papillose.

9. Leaf blades deeply and evenly suffused with maroon abaxially; floral bracts 2.0-3.0 cm long ..... *V. latissima*

9. Leaf blades green, occasionally suffused with maroon distally, abaxial surface never evenly suffused with maroon; floral bracts 1.0-1.8 (2.2) cm long.

10. Floral bracts 1.0-1.3 cm long; petals 2.3-3.1 cm long ..... *V.greenbergii*

10. Floral bracts 1.4-1.8 (2.2) cm long; petals 3.6-4.2 cm long ..... *V. umbrosa*

4. Lateral branches of the inflorescence not well developed, typically collaterally 2-flowered or, if proximal branches 3-flowered, then the inflorescence capitate or pendent; peduncles, rachises and pedicels highly reduced, or when developed then short and stout.

11. Floral bracts distinctly longer than the sepals.

12. Floral bracts at most 1.8 cm long; sepals 0.7-1.0 cm long; petals 1.7-1.9 cm long..... *V. kathyae*

12. Floral bracts greater than 2.0 cm in length; sepals greater than 1.3 cm in length; petals longer than 2.0 cm.

13. Sepals 2.0 cm long or longer; leaves brittle, thick-coriaceous, in cross-section the bundle sheaths not buttressed and not extending into the adaxial hypodermis; highly developed layer of extrafascicular sclerenchyma present in the adaxial hypodermis.

    14. Floral bracts 2.0-2.2 cm long, oblong to obovate, unkeeled or weakly keeled distally; petals 3.1-3.4 cm long ..... *V. capitata*

    14. Floral bracts 3.8-4.6 cm long, broadly elliptic or ovate to orbicular, strongly keeled; petals 3.8-4.3 cm long ..... *V. bracteosa*

13. Sepals at most 2.0 cm long and usually much shorter; leaves quite flexible; bundle sheaths buttressed, these extending well into the adaxial hypodermis, extrafascicular sclerenchyma wanting.

    15. Scape 16.0-26.0 cm long; leaves green, blades with fine longitudinal maroon lines proximally ..... *V. comata*

    15. Scape 29.0 cm long or longer, if shorter than the leaves then strongly suffused with maroon; leaves green or maroon frequently with wavy transverse lines.

        16. Leaves and bracts green, frequently suffused with reddish-brown wavy transverse lines ..... *V. hygrometrica*

        16. Leaves and bracts frequently suffused with maroon or red, or if green then with longitudinal maroon or red lines ..... *V. notata*

11. Floral bracts shorter than or about equaling the sepals or if slightly longer than the sepals, the inflorescence pendent.

    17. Inflorescence pendent; primary bracts brightly colored at anthesis; flowers diurnal.

        18. Floral bracts at most ½ as long as the sepals; sepals 2.2-3 cm long; leaf blades ligulate or rarely broadly triangular; at least 3.5 cm wide; known from the montane rainforest life zone ..... *V. uxoris*

        18. Floral bracts distinctly more than ½ as long as thesepals and usually about equal to the sepals; sepals less than 2.1 cm in length; leaf blades triangular or rarely subligulate, less than 3 cm wide; known from the premontane rainforest, wet forest and moist forest life zones.

            19. Inflorescence with 7 or more lateral branches; sepals 1.5-1.9 cm long; found in the premontane rainforest and wet forest life zones.

                20. Leaf blade and upper sheath area usually marked with conspicuous green or dark maroon wavy transverse lines; floral bracts green or rarely weakly suffused with pink; sepals green to yellow-green; primary bracts frequently geniculate-reflexed; sheaths of lower primary bracts 2.6-3.8 cm wide or, if rarely

narrower, then the leaves with obvious maroon transverse lines; most common in the premontane rainforest life zone ..... *V. leucophylla*

20. Leaf blade and upper sheath area unmarked, never with conspicuous green or maroon transverse lines; floral bracts deep pink to crimson; sepals deep red at anthesis; primary bracts subscalariform not geniculate-reflexed; sheaths of lower primary bracts 2-2.4 cm wide; most common in premontane wet forest life zone ..... *V. vietoris*

19. Inflorescence with 5 or fewer lateral branches; sepals 1.9-2.1 cm long; most common in the premontane moist forest life zone ..... *V. hainesiorum*

17. Inflorescence erect; flowers diurnal, crepuscular or nocturnal; primary bracts green, brightly colored or dried brown at anthesis.

21. Primary bracts pink to scarlet at anthesis; flowers diurnal, green to yellow green ..... *V. ororiensis*

21. Primary bracts green, maroon or dried brown at anthesis; flowers crepuscular or nocturnal or if rarely diurnal, then the primary bracts dried brown at anthesis.

22. Plants caulescent and producing tank-roots in the axils of the older leaves; leaves usually with longitudinal maroon lines at least proximally.

23. Inflorescence greater than 6.0 cm in length.

24. Floral bracts 1.6 cm long, lanceolate, occasionally wanting; longitudinal lines wanting ..... *V. picta*

24. Floral bracts 1.4 cm long or shorter ovate, oblong or cuniform, always present; longitudinal lines usually present ..... *V. williamsii*

23. Inflorescence 6.0 cm long or less in length.

25. Floral bracts 0.7-0.9 cm long; maroon lines broad, color not confined to the veins; inflorescences lax ..... *V. stenophylla*

25. Floral bracts 1.1-1.4 cm long; maroon lines very narrow, color apparently confined to bundle sheaths of veins; inflorescence subcapitate to dense cylindric ..... *V. attenuata*

22. Plants acaulescent or if caulescent, then tank-roots not produced; longitudinal colored lines infrequently produced.

26. Sepals (at least some) entirely maroon; leaf blades cinereously pubescent abaxially.

27. Floral bracts 1.5-1.7 cm long; petals 2.9 cm long; corolla tubular or campanulate at anthesis ..... *V. luis-gomezii*

27. Floral bracts 1.2 cm long or less; petals to 2.5 cm long; corolla tubular or campanulate at anthesis

28. Inflorescence 3.0-6.0 (9.0) cm long, with 8 or fewer lateral branches; floral bracts usually exceeding one-half the length of the sepals at anthesis; corolla campanulate ..... *V. balanophora*

28. Inflorescence 11.0-31.0 cm long, with considerably more than 10 lateral branches; usually less than the length of the sepals at anthesis floral bracts corolla tubular geniculate ..... *V. viridis*

26. Sepals green, olive-green or suffused with maroon marginally but not entirely maroon; abaxial leaf surfaces not obviously pubescent.

29. Flowers green, diurnal, petals 2.6 cm long or less, corolla tubular at anthesis ..... *V. ororiensis*

29. Flower white or greenish white, nocturnal, petals 3.1-5.4 cm long.

30. Corollas strongly zygomorphic at anthesis; style 2.4-3.7 cm long; sepals elliptic to obovate; mature capsules to 4.3 cm long ..... *V. nephrolepis*

30. Corollas subtubular at anthesis; style 1.7-2.1 cm long; sepals frequently suborbicular; mature capsules 4.9-5.3 cm long ..... *V. lyman-smithii*

1. ***Vriesea leptopoda*** L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953.

Thecophyllum rubrum Mez & Werckle in Mez, Bull. Herb. Boiss. ser II. 4: 878. 1904, not *Vriesea rubra* Beer, 1857.
TYPE: COSTA RICA: *Werckle, Bromel. Costaric. 100* (HOLOTYPE: B!; ISOTYPE: GH).

Epiphytic or terrestrial, acaulescent. LEAVES in a spreading rosette, 38.0-55.0 (62.0) cm long; *blades* 14.0-31.0 cm long and 5.0-8.0 cm wide, green or green suffused with purple, especially on the lower surface or near the apices, ligulate, apex acute to rounded and acuminate; *sheaths* 19.0-27.0 (31.0) cm long and 7.0-12.0 cm wide, pale green drying to light brown with a coating of cinereous trichomes, frequently with a castaneous band near the base, elliptic to weakly obovate. SCAPE erect or curved-erect, 60.0-65.0 cm long and 0.4-1.2 cm in diameter; *bracts* erect, 3.5-4.5 cm long and (1.9) 2.2-3.2 (3.7) cm wide, green the middle and upper soon drying brown, exceeding or about equaling the internodes, ovate to elliptic, apex acute to acuminate. INFLORESCENCE erect, glabrous, (23.5) 35.0-55.0 (67.0) cm long and 8.0-12.0 cm in diameter; *primary bracts* 3.5-4.2 cm long and (1.6) 2.0-2.8 (3.7) cm wide, dried brown, ovate to

elliptic, apex acute to acuminate, LATERAL BRANCHES 3.5-6.7 cm long, 5-to 8-flowered, peduncle 0.4-0.7 (1.1) cm long, rachis 3.1-4.7 (5.5) cm long. FLOWERS 1.7-2.0 cm pedicellate; *floral bracts* 1.4-1.8 cm long and 0.5-0.9 (1.2) cm wide, dried brown, surface nerved, frequently short tuberculate, keel usually present as a narrow longitudinal thickening, occasionally confined to the distal portion or absent, elliptic to ovate, navicular, apex acute or torn and appearing bifid; *sepals* 1.4-1.6 cm long and 0.8-1.1 cm wide, coriaceous, green or green suffused with maroon drying to brown or yellow-brown, elliptic to obovate, apex obtuse to rounded; *petals* 2.5-2.7 cm long and 1.2-1.3 cm wide, white, elliptic; *appendages* 0.5-0.6 cm long and 0.2-0.3 cm wide; *stamens* in a hood configuration over style, anthers not connivent, filaments 1.4-1.7 cm long, anthers 0.5-0.6 cm long; *ovary* 0.5-0.6 cm long and 0.3-0.4 cm in diameter, style about 1.9 cm long, exserted beyond the staminal hood; *capsules* 2.2 cm long and about 0.6 cm in diameter, fusiform, castaneous.

PHENOLOGY: Flowering specimens have been collected in March and May.

DISTRIBUTION AND HABITAT: Costa Rica and northwestern Panamá between 1600-2300 m in the premontane and lower montane rain forest life zones.

DISCUSSION: Prior to my collections *Vriesea leptopoda* was only known from the type material. Since the inflorescence of the type specimen is either immature or aborted and only the inner rosette leaves are present, exact interpretation of this specimen was difficult. However, its broad leaves and the nature of the pedicels and floral bracts, when taken together, are a unique combination of characters which eliminates other interpretations. Leaves of this taxon, which are green suffused with maroon abaxially, form a broad, spreading rosette. The inflorescence is erect, with well developed lateral branches. Floral bracts of this taxon are membranaceous and about equal to or shorter than the slender, elongate pedicels. The white, campanulate, nocturnal flowers of *V. leptopoda* are characteristically downwardly secund at anthesis.

In vegetative condition, *V. leptopoda* can be easily confused with *V. latissima*. The features that distinguish these taxa are presented under *V. latissima*. Phenetically, *V. leptopoda* is most similar to *V. pedicellata*. In both taxa the flowers are slenderly pedicellate, the floral bracts are membranaceous and shorter than, or equal to, the pedicels and the flowers are white, campanulate and nocturnal. These taxa are readily separated by pedicel length, floral bract size, and sepal and petal size.

SPECIMENS EXAMINED: COSTA RICA: CARTAGO PROVINCE: Aserí, on tree in cloud forest, 19 March 1966, *L. B. Smith,* et al. *15324*. Region between Cascajal and ca 8 km northeast on CR Highway 216 or about 6 km slightly south of due east from Alto de La Palma, 1600-1800 m, 23 August 1975, *Utley & Utley 2925* (DUKE). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: ca 17 km south of El Empalme on the Interamerican Highway, ca 2600m, 17 March 1975 (grown in hort., pressed 22 May 1975), *Utley & Utley 2003* (DUKE). HEREDIA: Between the junction of Costa Rican highways 9 and 120 and 3 km south on Hwy. 9, 1900-2100 m, 11 May 1975, *Utley and Utley 2486* (CR), 27 March 1976, *Utley & Utley 4374* (NOLS), 3 May 1976, *Utley & Utley 4695* (DUKE), secondary road north of CR Hwy. 113 connecting with Calle Gallito, saddle area between Cerro Chompipe and the southeast flank of Volcan Barba, 2000-2100 m, 8 December 1975, *Utley & Utley 3581* (NOLS) & 3582 (DUKE). SAN JOSÉ: Cerros de Escazu (Cedral) approach to and summit of Cerro Daser, 2220-2318 m, 25 May 1975, *Utley & Utley 2517* (DUKE). PANAMÁ: CHIRIQUÍ PROVINCE: Bajo Chorro, 17 February 1938, *Davidson 307* (F).

2. *Vriesea pedicellata* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953 Fig. 17.

Thecophyllum pedicellatum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 3: 136. 1903.
TYPE: COSTA RICA: province not given: near Cartago, elevation 1200-1600 m, Werckle *in Inst. Phys.-Geogr. Costar. 16197* (HOLOTYPE B!, photograph US!)

Thecophyllum violascens Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 877. 1904.
TYPE: COSTA RICA: province not given, near La Palma, *Werckle Bromel. Costaric. 43, 91.*
(LECTOTYPE: *Werckle Bromel. Costaric. 43,* B!, photograph US! SYNTYPE: *Werckle Bromel. Cosraric. 91,*B!, photograph US!).

Thecophyllum turbinatum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 1122. 1904.
TYPE: COSTA RICA: location not given, *Werckle Bromel. Costaric. 116* (HOLOTYPE: B!, photograph US!, ISOTYPE: GH).

Vriesea violascens (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403.1953.

Vriesea turbinata (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403.1953.

Epiphytic or terrestrial, acaulescent. LEAVES in a spreading to subascending rosette, 19.0-47.0 (57.0) cm long; *blades* (7.0) 17.0-34.0 (41.0) cm long and (2.0) 2.4-5.3 cm wide, green usually suffused with purple or reddish-maroon abaxially or infrequently both surfaces, frequently with longitudinal purple or maroon lines, ligulate to subligulate or broadly triangular, apex acute to acuminate or broadly acute to rounded and short acuminate; *sheaths* (7.0) 9.0-20.0 (22.0) cm long and 3.4-7.0 (8.4) cm wide, drying pale green with a coating of cinereous trichomes, usually suffused with longitudinal purple lines or purple to red distally, elliptic to ovate in outline. SCAPE erect to curved erect, (18.0) 24.0-50.0 (60.0) cm long and 0.2-0.5 (0.8) cm in diameter; *bracts* 3.3-9.0 (12.8) cm long and 1.3-3.9 cm wide, blade and sheath areas not clearly delimited, pale green, frequently suffused with longitudinal purple or maroon stripes, erect and clasping in the sheath area, divergent in distal portion of blade, sheath elliptic to ovate, blades triangular, apex acute to acuminate. INFLORESCENCE erect (6.0) 10.0-38.0 (54.0) cm long and (4.0) 6.0-11.0 cm in diameter, cylindric, rachis green or suffused vwith purple; *primary bracts* (3.1) 3.6-8.0 (10.4) cm long and 1.5-3.5 cm wide, sheath and blade areas not clearly delimited, green frequently suffused with purple, drying brown at anthesis, sheaths ovate to elliptic or rarely obovate, blades triangular to elongatetriangular, apex acute to acuminate. LATERAL BRANCHES spreading to ascending (0.3) 0.9-2.3 (3.3) cm long, 2-5 (6) flowered, flowers racemose, peduncles wanting to 0.3 (0.6) cm long, rachis 0.3-2.5 cm long. FLOWERS (0.6) 0.8-1.9 (2.2) cm pedicellate; *floral bracts* 0.4-0.8 cm long and 0.3-0.6 cm wide, drying pale brown at anthesis, membranous, glabrous, finely nerved, even or slightly keeled, ovate to elliptic or rarely oblong, apex acute to obtuse or rounded; *sepals* 0.8-1.2 cm long and 0.5-0.8 (1.0) cm wide, green or purple drying olive-green to castaneous, coriaceous, glabrous, elliptic to obovate, apex obtuse to rounded, frequently torn incised; *petals* 1.8-2.1 (2.4) cm long and 0.9-1.1 (1.4) cm wide, white occasionally lightly suffused with maroon marginally and apically, obovate; *appendages* 0.3 cm long and 0.1-1.2 cm wide; *stamens* loosely arranged over the gynoe-

cium, anthers not connivent by their lateral margins, filaments 1.1-1.7 cm long, anthers 0.3-0.4 cm long; *ovary* 0.5 cm long and 0.25-0.35 cm in diameter, style 0.7-0.9 (1.6) cm long; *capsules* 2.0-2.4 cm long and 0.4-0.7 cm in diameter, castaneous, fusiform.

PHENOLOGY: Flowering specimens have been collected in December, and January but flowering likely occurs during other months as well.

DISTRIBUTION AND HABITAT: Known from Costa Rica, Nicaragua and Honduras between 900-2100 m in the lower montane and premontane rain forest life zones and the lower montane and premontane wet forest life zones.

DISCUSSION: *V. pedicellata* is a commonly encountered, but not often collected taxon. Of the thecophylloid vrieseas, it is the most variable species, exhibiting much greater variability than either *V.nephrolepis* or *V. ororiensis*. Variation has been observed in size and general robustness, leaf coloration and markings, the degree of development of the lateral branches of the inflorescence and the number of flowers. Within a single population, the inflorescence can vary from 6-10 cm in length to over 50 cm. This is correlated with both the size of the flowering individuals and the degree of development of the lateral branches. Smaller plants tend to have shorter inflorescences with fewer flowered lateral branches, while larger individuals have extremely robust inflorescences with as many as five or six flowers per lateral branch. Variation in robustness is accompanied by, but apparently not correlated with, a great variation in leaf color and markings. Leaves of *V. pedicellata* range from green to maroon or deep red-purple and may be unlined, weakly lined or strongly lined throughout the leaf blade. Although *V. pedicellata* is a highly variable taxon, individuals are united by a series of common characters, including ligulate leaves and membranaceous floral bracts that are generally shorter than the pedicels. The white, campanulate flowers of this taxon are nocturnal.

Figs. 17. *Vriesea pedicellata* inflorescence

The variation encompassed by *V. pedicellata* was not recognized by Mez (1933-1934) because the fragmentary collections available at that time permitted little insight into this difficult species. As a result, Mez (1904) described *Thecophyllum violescens*, a species he distinguished from *T. pedicellatum* on the basis of a lack of development of the lateral branches of the inflorescences and only two flowers per axil. Because the development of lateral branches of *V. pedicellata* is a variable character displaying many intermediate forms, it is impossible to maintain *V. violescens* using this criterion. Because flower number varies and is dependent on the development of the lateral branches, it cannot be used to characterize *V. violescens*. I consider *V. violescens* to be well within the variation I observed in *V. pedicellata* popu-

lations and cannot maintain it as a distinct species. *Vriesea turbinata,* which I also consider to be conspecific with *V. pedicellata*, is represented by very fragmentary material. The scape is entirely wanting from the type and it is even doubtful that the entire post-fruiting inflorescence has been preserved. Moreover the leaf material is difficult to interpret, being either badly decomposed, mutilated or from the central portion of the rosette and consequently not representative. In light of the poor condition of this specimen, I could not reach an unequivocal decision regarding the disposition of the binomial, *V. turbinata.* However, the texture and size of the floral bracts and pedicel length in conjunction with the general form of lateral branches of the inflorescence conforms with that of *V. pedicellata.* In light of the available information regarding these taxa, I feel that *V. turbinata* should be considered a synonym of *V. pedicellata.*

Several anomalous collections have been made of *V. pedicellata* at higher elevations in the Talamanca Mountains between El Empalme and Villa Mills *(Utley & Utley 1518, 2763, 2754 and 5266).* In all these collections the scape bracts are about equal to the internodes and flowers are frequently subtended by enlarged floral bracts. When further collections are available, this element may prove to be a distinct species.

V. pedicellata is phenetically most similar to *V. leptopoda.* The characters distinguishing these two taxa are discussed under *V. leptopoda.*

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE:Viento Fresco, 13 February 1926, *Standley & Ruben Torres R. 48020* (US); north of San Ramón, region from Los Angeles Norte to about 12 km north of La Balsa de San Ramón, 15 December 1974, *Utley & Utley 1653* (NOLS) & *1670* (DUKE); 8 August 1975, *Utley & Utley 2768* (DUKE) & *2770* (CR); 27 January 1976; *Utley & Utley 3794* (K) & *3795* (DUKE). CARTAGO PROVINCE: 10 miles south of Cartago on the Interamerican Highway, Talamanca Mountains, 10 July 1962, *Haines & Haines 687* (US); 21 miles south of Cartago on Interamerican Highway, 10 July 1962, *Haines & Haines 701* (US) & *702* (US); 16 miles south of Cartago on Interamerican Highway, 17 July 1962, *Haines & Haines 719* (US); 22 miles south of Cartago on Interamerican Highway, 17 July 1962, *Haines & Haines 723* (US),*729* (US) & *732* (US); 29 miles south of Cartago on Interamerican Highway, 19 July 1962, *Haines & Haines 734* (US); Cerro de La Carpintera, February 1924, *Standley 34304* (US); north of El Muneco, 5 April 1974, *Utley & Utley 785* (DUKE); Tapantí Hydroelectric Project about 7-14 km southeast of Orosí on slopes above the Río Grande de Orosí, 13 December 1974, *Utley & Utley 1605* (DUKE) & *1610* (F); 14 April 1975, *Utley & Utley 2109* (DUKE), *2110*, (MO) & *2111* (CR); 5-6 miles south of San Isidro de Cartago, 8 June 1975, *Utley & Utley 2536* (DUKE), *2540* (US), *2541* (MICH) & *2542* (F); Tapantí Hydroelectric Project about 7-14 km southeast of Orosí, 5 December 1975, *Utley & Utley 3415* (B) &*3420* (MO), 3422 (CR), *3424* (F) & *3435* (DUKE); 22 March 1976, *Utley & Utley 4357* (DUKE), *4358* (US), *4359* (CR), *4361* (DUKE), *4362* (CAS), *4365* (MO), *4366* (NOLS) & *4367* (DUKE). BORDER OF-CARTAGO AND SAN JOSE PROVINCES: along the Interamerican Highway about 20 km south of Cartago, in the vicinity of Casa Mata, 17 March 1975, *Utley & Utley 1995* (DUKE); 3 August 1975, *Utley & Utley 2760* (DUKE); HEREDIA PROVINCE: 2-3 km southeast of the junction of highways 9 and 120 on Hwy. 9, 27 March 1976, *Utley & Utley 4375* (DUKE) & *4385* (F). SAN JOSE PROVINCE: San Jerónimo, March 1909, *Biolley fil. 17365* (US); La Hondura, on tree, 2-4 March 1924, *Standley 36220* (US); Alto de La Palma, north of San Jeronimo, 12 January 1974, *Utley & Utley 617* (DUKE); 15 February

1974, *Utley & Utley 625* (CR); 1 June 1974 *Utley & Utley 891* (US); 17 October 1974, *Utley & Utley 1407* (NOLS); 15 April 1975, *Utley & Utley 2136* (CAS), *2147* (NY), *2149* (CR), *2151* (DUKE) & *2152* (GH); 9 June 1975, *Utley & Utley 2559* (DUKE) & *2560* (NOLS); 19 June 1975, *Utley & Utley 2564* (DUKE) & *2569* (CR); vicinity of Bajo La Hondura, north of Alto de La Palma, 23 October 1975, *Utley & Utley 3186* (DUKE); about 5 km northeast of San Isidro de Heredia on Calle Yerbabuena, 3 April 1976, *Utley & Utley 4465* (DUKE) *4467* (US) & *4468* (CR); between Alto de La Palma and Bajo La Hondura or 6-8km northeast of San Jerónimo, 6 April 1976, *Utley & Utley 4514* (DUKE); at Cascajal about 3 km north of Las Nubes on Hwy. 216, 3 July 1976, *Utley & Utley 5251* (DUKE). PUNTARENAS-PROVINCE: Monteverde, 17 km west of Las Juntas de Abangares, in the cloud forest above the Quaker settlement, 27 January 1975, *Utley & Utley 1883* (DUKE, CR, US). HONDURAS: FRANCISCO MORAZÁN: Montaña Uyuca, off km 25, Tegucigalpa-Zamorano highway, 19 July 1964, *Gilmartin 998* (US). NICARAGUA: DEPARTMENT OF JINOTEGA: Cordillera Central de Nicaragua above and east of Jinotega, 20 February 1963, *Williams,* et al. *24761* (F). DEPARTMENT OF MATAGALPA: cloud forest area at Disparate de Potter, near Sta. María de Ostuma, 20 & 24 February 1963, *Williams,* et al. *25062* (F), 15 February 1965, *Williams*, et al. *27681* (F).

3. *Vriesea diffusa* L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

Thecophyllum laxum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 1123. 1904, not *Vriesea laxa* Mez, 1896.

TYPE :COSTA RICA: without further location, *Werckle Bromel. Costaric. 90* (HOLOTYPE: B!, photograph US!).

Epiphytic or terrestrial, acaulescent. LEAVES in a spreading to subascending rosette, (13.5) 17.0-25.0 cm long; *blades* 8.0-13.5 (15.0) cm long and 1.7-3.5 cm wide, green with a dense coat of appressed, cinereous trichomes on the abaxial surface, frequently with longitudinal maroon lines proximally, ligulate or subligulate to broadly triangular, apex acute to acuminate; *sheaths* (4.9) 5.5-11.5 (13.0) cm long and 2.6-4.6 cm wide, pale green with longitudinal maroon lines, frequently suffused with maroon centrally. SCAPE erect or curved-erect, 20.0-32.0 (42.5) cm long and 0.2-0.3 cm in diameter; *bracts* 1.8-2.8 (3.4) cm long and 0.7-1.6 cm wide, erect-clasping, occasionally spreading apically, green drying to brown, frequently with longitudinal maroon markings in the lower blade, much shorter than the internodes. INFLORESCENCE erect, (3.5) 5.5-16.0 cm long and 2.0-6.0 cm in diameter, more or less cylindrical; *primary bracts* 1.2-2.4 cm long and 0.6-1.3 (2.0) cm wide, green drying brown, frequently with longitudinal maroon lines, apex acuminate. LATERAL BRANCHES spreading or ascending to rarely suberect, (1.8) 2.2-4.2 cm long, (1) 2 (3)- flowered, these collateral to spicate, peduncle (1.6) 2.2-3.6 cm long, rachis wanting or 0.5-0.9 (1.3) cm long. FLOWERS 0.3-0.4 cm pedicellate; *floral bracts* 0.5-0.7 cm long and 0.5-0.7 cm wide, brown, chartaceous, nerved, midvein frequently thickened and the bract slightly keeled, ovate to subtriangular, apex acute to obtuse or rounded and minutely apiculate; *sepals* 0.8-1.0 cm long and 0.5-0.8 cm wide, light castaneous to olive-brown, coriaceous, elliptic, apex rounded; *petals* 1.5-1.6 cm long and 0.8-0.9 cm wide, white, obovate; *appendages* 0.3 cm long and 0.1-0.15 cm wide; *stamens* in hood configuration over the gynoecium, filaments 1.0-1.1 cm long, anthers 0.2-0.3 cm long; *capsules* (1.6) 2.0-2.7 cm long and 0.4-0.6 cm in diameter, castaneous, fusiform.

PHENOLOGY: Flowering specimens collected during June and August.

DISTRIBUTION AND HABITAT: Known from Costa Rica and Panama between 900-1500 m in the premontane rain forest life zone.

DISCUSSION: The characters that distinguish *Vriesea diffusa* are pale green leaves with green blades that are frequently longitudinally lined with purple proximally and pale green sheaths with longitudinal purple striations. Its slender scape (0.2-0.3 cm in diameter) bears scape bracts that are usually much shorter than the internodes. The peduncles of the lateral branches are unusually long (2.2-3.6 cm) while the floral bracts exceed the pedicels. The flowers of *V. diffusa* are white, campanulate and nocturnal, resembling in general morphology those of both *V. triflora* and *V. pedicellata.*

Based on a number of characters, *V. diffusa* appears to be most closely related to *V. triflora.* Both taxa characteristically display papillose induments on the inflorescence rachis, peduncles and pedicels, a feature not encountered among other thecophylloid vrieseas. Inflorescence form in both taxa is very similar although inflorescences of *V. triflora* are much larger and more fully developed than those of *V. diffusa.* The two taxa are readily separable on the basis of a number of characters. Both floral bracts and petals are shorter in *V. diffusa* than in *V. triflora.* In the vegetative condition, the taxa may be distinguished from each other on basis of leaf markings. Leaves of *V. triflora* characteristically have proximal wavy transverse lines, while those of *V. diffusa* are longitudinal.

Both *V. triflora* and *V. diffusa* are probably most closely related to *V. pedicellata* and *V. leptopoda,* from which they are easily distinguished by their densely papillose branches as well as a suite of other characters.

From the available collections, *V. diffusa* appears to have a more widespread distribution than *V. triflora.* This may be a reflection of its occurrence at lower elevations (900 m) than *V. triflora (1400 m).* However, much of the Atlantic watershed of both Costa Rica and Panama is poorly collected and as these areas become better known floristically, the distribution of *V. triflora* will possibly be expanded.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA: north of San Ramón, the region from La Balsa to about 4.5 km north, *Utley & Utley 1857* (DUKE, US, F, CR, MO, K, CAS, GH, MICH, NOLS, CR); between La Balsa de San Ramón and the Río Cataratas or about 12 km north of La Balsa, *Utley & Utley 3740* (DUKE); about 4 km north of La Balsa de San Ramón on the road leading to the Atlantic watershed, *Utley & Utley 4121* (DUKE). BORDER OF ALAJUELA AND HEREDIA PROVINCES: vicinity of Colonia Virgen del Socorro, or about 3-6 km east of Cariblanco, *Utley & Utley 2880* (NOLS) & 2881 (DUKE). CARTAGO: Tapantí Hydroelectric Project, between 7 and 12 km south of the bridge over the Rio Grande de Orosí at Tapantí, *Utley & Utley 3410* (DUKE). SAN JOSÉ: La Hondura, *Standley & Valerio 51912* (US); La Palma, *Werckle 9* (US). REPUBLIC OF PANAMA: PANAMA: Cerro Campana, trail to summit, *Dressler 5141* (US).

4. *Vriesea triflora* L. B. Smith & Pitt. J. Wash. Acad. Sci 43: 403. 1953.

Thecophyllum panniculatum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 1128. 1904, not *Vriesea paniculata* Mez. 1896.

TYPE: COSTA RICA: SAN JOSÉ: la Palma, *Werckle 55* (HOLOTYPE: B!, photograph US!; ISOTYPE: B!; photograph US!).

Epiphytic or terrestrial, acaulescent.

LEAVES in a spreading rosette, (23.0) 26.0-34.0 cm long; *blades* (10.0) 13.0-18.0 cm long and 2.8-4.2 (4.8) cm wide, green strongly suffused with wavy maroon cross-bands proximally, these more pronounced on the abaxial surface, ligulate to subtriangular with an acute to acuminate apex; *sheaths* (12.0) 13.0-15.5 (16.5) cm long and 4.0-6.0 cm wide, green densely suffused with maroon wavy cross-bands and longitudinal maroon lines, occasionally with a castaneous band at the base, covered with a coating of pale brown trichomes, elliptic. SCAPE erect, (31.5) 36.0-46.0 cm long and about 0.3 cm in diameter; *bracts* frequently spreading distally, 2.0-3.0 cm long and 1.0-2.0 cm wide, green frequently suffused with maroon and maroon longitudinal lines proximally and with maroon spots or transverse lines distally, erect, middle and upper bracts much shorter than the internodes. INFLORESCENCE erect, (29.0) 38.0-49.0 cm long and (11.0) 15.0-20.0 cm in diameter, cylindrical to conical in shape, rachis frequently sinuous distally, the surface densely papillose, purple-green in color with a metallic sheen; *primary bracts* 1.8-2.5 cm long and 0.9-1.6 cm wide, green with longitudinal maroon lines and occasionally with maroon spots or transverse lines distally, apex acuminate to acute. LATERAL BRANCHES spreading, the distal portion becoming ascending and the fertile portion suberect, 8.0-14.0 cm long, racemosely (2) 3 (5)-flowered with a non-functional terminal bud, flowers frequently secund, peduncles (5.6) 7.0-10.0 cm long, rachis 1.8-4.4 cm long. FLOWERS 0.1-0.5 cm pedicellate; *floral bracts* 0.9-1.2 cm long and 0.7-1.2 cm wide, brown at anthesis, chartaceous, finely nerved, the central vein frequently thickened distally, ovate or orbicular, apex rounded frequently apiculate, often torn and appearing incised; *sepals* 0.7-1.2 cm long and 0.6-0.9 cm wide, castaneous, coriaceous, elliptic, apex acute to rounded; *petals* 1.9-2.0 cm long and 1.0-1.1 cm wide, white, obovate; *appendages* 0.3-0.4 cm long and 0.1-0.2 cm wide; *stamens* in a hood configuration over the gynoecium, anthers laterally connivent, filaments 1.4 cm long, anthers 0.4 cm long; *ovary* 0.4 cm long and 0.3 cm in diameter, style 1.2 cm long; *capsules* 1.5-2.5 cm long and about 0.5 cm in diameter, fusiform.

PHENOLOGY: Flowering specimens collected in June.

DISTRIBUTION AND HABITAT: Known from Costa Rica between 1400-1700 m in the premontane rain forest life zone and possibly extending slightly into the lower montane rain forest.

DISCUSSION: Until my recent collections from Costa Rica, *Vriesea triflora* was poorly represented in herbaria. In both the vegetative and flowering condition this taxon is difficult to distinguish from surrounding vegetation. In contrast to other thecophylloid vrieseas, the inflorescences of this taxon, although large, are slender and inconspicuous and lack large scape and primary bracts.

Vriesea triflora is characterized by ligulate leaves with proximal, wavy transverse lines and an erect scape with bracts much shorter than the internodes. Its inflorescence is lax, with a characteristically papillose rachis. The lateral branches of the inflorescence are elongate and also densely papillose. The flowers of this taxon are white, nocturnal and campanulate, and very similar to those encountered in *V. pedicellata* and *V. diffusa*. Although *V. triflora* shares this common floral syndrome with *V. pedicellata*, its closest affinities are clearly with *V. diffusa*. This relationship is discussed in greater detail under *V. diffusa*.

SPECIMENS EXAMINED: COSTA RICA: CARTAGO PROVINCE: Tapantí Hydroelectric Project, 7-12 km south of the bridge over the Río Grande de Orosí at Tapantí, 5 December 1975, *Utley & Utley 3417* (DUKE) & *3434*(CR); 25 June 1976, *Utley & Utley 5160* (DUKE), *5162* (US),

5163 (F), *5193* (NOLS), *5194* (MO), *5195* (DUKE), *5196* (CR), *5197* (NOLS),*5198 (CR), 5199* (F), *5200* (CAS), & *5201* (NY). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: about 5 km northeast of San Isidro de Heredia along the Río Para Blanco, 28 May, 1976, *Utley & Utley 5097* (DUKE). SAN JOSÉ PROVINCE: 4 km north of Cascajal on Hwy. 216, southwestern slopes of Volcán Irazu, 3 July 1976, *Utley & Utley 5257* (DUKE); La Palma, *Werckle 11* (US). COSTA RICA: without further location: September 1955, *Lankester, C. s.n.* (US).

5. *Vriesea greenbergii* Utley, sp. nov. Fig. 18

A *V. umbrosa* L. B. Smith, cui valde affinis, sepalis et petalis minoribus, follis rotundatis abrupte acutis differt.

Epiphytic or terrestrial, acaulescent. LEAVES in a spreading to subspreading rosette, 32.0-40.0 (45.0) cm long; *blades* 15.0-22.0 (28.0) cm long and 3.8-5.8 (6.6) cm wide, green occasionally suffused with maroon distally, ligulate, apex acute or acuminate to rounded and abruptly acute; *sheaths* 12.0-20.0 (26.8) cm long and (3.1) 4.6-6.8 (8.0) cm wide, pale green drying light brown with a coating of brownish trichomes, usually with a dark castaneous band near base and occasionally with a trace of longitudinal lines, elliptic. SCAPE erect or curved-erect, (33.0) 43.0-49.0 cm long and 0.2-0.4 (0.7) cm in diameter; *bracts* clasping-erect, 3.0-4.8 cm long and 1.8-3.4 (4.0) cm wide, green to green suffused with maroon distally, usually exceeding the internodes but occasionally equaling or slightly shorter than the internodes. INFLORESCENCE erect, (7.0) 13.0-20.0 (32.5) cm long and 5.0-11.0 (14.0) cm in diameter,laxly cylindric; *primary bracts* 2.4-4.2 cm long and 2.0-3.6 cm wide, green frequently suffused with maroon distally, ovate to elliptic, apex acute or acuminate. LATERAL BRANCHES spreading to subascending, (1.0) 1.8-3.2 (5.4) cm long, racemosely 2-to 3 (5)-flowered, rachis (0.2) 1.0-2.5 (4.2) cm long. FLOWERS 0.5-1.2 cm pedicellate; *floral bracts* 1.0-1.3 cm long and 0.9-1.2 (1.5) cm wide, green occasionally suffused with maroon drying to brown, subcoriaceous, ovate to broadly elliptic or oblong, navicular, apex acute to obtuse or rounded and short acuminate; *sepals* (1.0) 1.3-1.7 cm long and 0.9-1.1 (1.3) cm wide, green drying to brown, coriaceous, elliptic to obovate; *petals* 2.3-3.1 cm long and 1.1-1.5 cm wide, white, obovate; *appendages* 0.3-1.4 cm long and 0.15-0.2 cm wide; *stamens* in a hood configuration over the gynoecium, filaments 1.7-2.3 cm long, anthers 0.4-0.5 cm long; *ovary* 0.4-0.5 cm long and 0.3 cm in diameter, style 1.2-2.0 cm long; *capsules* about 3.5 cm long and 0.8 cm wide, fusiform.

TYPE: COSTA RICA: ALAJUELA PROVINCE: north of San Ramón, between La Balsa de San Ramón and the Río Cataratas or about 12 km north of La Balsa, elev. 900-1000 m, 27 January 1976, *Utley & Utley 3741* (HOLOTYPE: DUKE! ISOTYPES: CR!, DUKE!, F!, US!).

PHENOLOGY: flowering specimens have been collected in August, December, January and February, with the peak occurring in January and February.

DISTRIBUTION AND HABITAT: Endemic to Costa Rica, occurring between 800-1500 m in the premontane rain forest life zone.

DISCUSSION: *Vriesea greenbergii* is an easily recognized taxon that is distinguished by its green, usually unmarked leaves borne in a spreading rosette, by well developed lateral branches (1.8-3.2 cm long) and by white, nocturnal flowers with weakly zygomorphic corollas. Although *V. greenbergii* is very abundant in the type locality, it was never encountered in similar habitats in other parts of Costa Rica. Future collecting may, however, reveal a more widespread

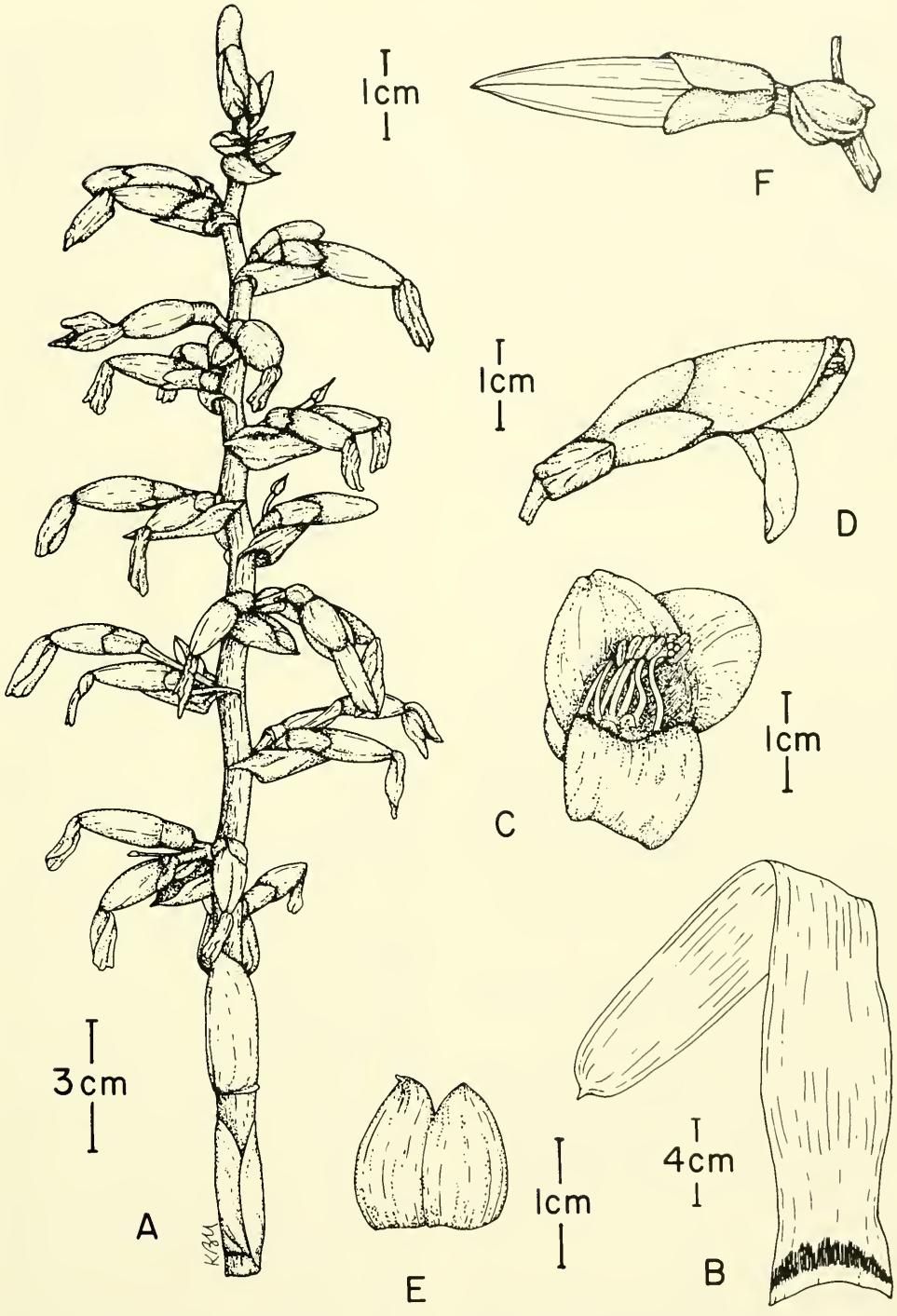


Fig. 18. *Vriesea greenbergii.* A. Inflorescence and upper portion of the scape; B. Leaf; C. Flower; D. Flower with sepals and floral bract; E. Floral bract, torn apically; F. Fruit with sepals and floral bract. A, B, F, from *(Utley & Utley 3741)* C, D, E, from *(Utley & Utley 1688).*

distribution

Vriesea greenbergii is most closely related to *V. umbrosa*. Although these taxa share a common floral morphology, no pleasant fragrance was observed in the flowers of *V. greenbergii*. *V. greenbergii* differs from *V. umbrosa* in floral bract length, petal length and leaf shape. Leaf blades of *V. greenbergii* are rounded and abruptly acute apically, in contrast to the acute to acuminate leaf apices of *V. umbrosa*. These species also have different elevational distributions, with *V. umbrosa* occurring between 1200 and 1900 m and *V. greenbergii* between 800 and 1200 m. Both species share characters in common with *V. latissima*, which are discussed under this latter taxon.

ETYMOLOGY: This species is named in honor of the noted aquatic plant horticulturist, Mr. Albert Greenberg, of Tampa, Florida.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: north of San Ramón, region between Los Angeles Norte and about 7 km north, 15 December 1974, *Utley & Utley 1688* (DUKE) & *1689* (CR); between La Balsa de San Ramón and 12 to 13 km north, 8 February 1976, *Utley & Utley 4059* (NOLS), *4064* (US), *4122* (CR), *4123* (GH), *4124* (DUKE), *4125* (MO) & *4126* (NY).

6. *Vriesea umbrosa* L. B. Smith, Phytologia 23: 328-329. 1974.

TYPE: COSTA RICA: SAN JOSÉ: La Palma area, northeast of San Jeronimo, above the La Hondura valley. elev. 1500 m. Burger & Stolze 5333 (HOLOTYPE: US!; ISOTYPES: F!, CR!).

Epiphytic or terrestrial, acaulescent. LEAVES in a speading to subascending rosette, (45.0) 51.0-80.0 (93.0) cm long; *blades* (25.0) 33.0-53.0 (63.5) cm long and (3.6) 4.8-6.4 cm wide, green ligulate to subligulate or long triangular, apex acute to acuminate; *sheaths* 16.0-26.0 (29.0) cm long and 5.0-8.5 (10.0) cm wide, pale green drying to light brown with a coating of brownish grey to cinereous trichomes, elliptic. blending gradually into the blade. SCAPE erect or curved-erect (47.0) 55.0-68.0 (77.0) cm long and 0.4-0.8 cm in diameter; *bracts* (4.0) 5.0-8.0 (9.0) cm long and 3.0-5.2 cm wide, green the middle and upper soon drying brown, clasping erect, divergent to spreading distally, exceeding the internodes, ovate to broadly elliptic or suborbicular, apex acute to acuminate. INFLORESCENCE erect, (17.0) 21.0-39.0 (51.0) cm long and 6.0-10.0 cm in diameter, cylindric, the surface glabrous with minute black linear punctulae; *primary bracts* (3.5) 4.0-6.0 (7.6) cm long and 3.0-5.2 cm wide, green soon drying brown, ovate to elliptic, broad-elliptic or suborbicular, apex acute to acuminate. LATERAL-BRANCHES spreading, to subspreading, (1.0) 2.0-3.4 cm long, racemosely (2) 4-to 5-flowered peduncles 0.1-0.6 (0.9) cm long, and the rachis (0.6) 1.2-2.2 (2.8) cm long. FLOWERS 0.3-0.8 (1.0) cm pedicellate; *floral bracts* 1.4-1.8 (2.2) cm long and 1.1-2.2 cm wide, dried brown, subcoriaceous, surface even to indistinctly nerved, frequently with minute raised, clear to light brown, puncutulae, usually with a more or less thickened central area along which the bracts tend to fold, ovate to elliptic or suborbicular, apex acute to obtuse or rounded, at times minutely incised due to tearing; *sepals* 1.4-2.0 cm long and 0.9-1.3 cm wide, green to yellow-green drying to light brown or castaneous, coriaceous, elliptic to obovate, the apex acute to obtuse rounded, at times minutely incised due to tearing; *petals* 3.6-4.2 cm long and 1.6-2.1 cm wide, white, tipped with maroon; *appendages* 0.4-0.6 cm long and 0.2-0.25 cm wide, *stamens* coalescent by the lateral margins of the anthers into a hood over the gynoecium, filaments 2.4-3.4 cm long, anthers 0.7-0.9 cm long; *ovary* 0.5-0.7 cm long and 0.3-0.4 cm in diameter, style

3.0-3.4 cm long; *capsules* about 3.5 cm long and 0.7 cm in diameter, fusiform.

PHENOLOGY: Flowering specimens have been collected during April and May.

DISTRIBUTION AND HABITAT: Known from Costa Rica and Panamá between 1200-1900 m in the lower montane and premontane wet forest life zones and lower montane and premontane rain forest life zone.

DISCUSSION: *Vriesea umbrosa* was only recently described by Smith (1974) from fragmentary material. It is a distinctive species with green, unmarked leaves in a generally spreading rosette. The inflorescence of *V. umbrosa* is erect, with well developed lateral branches bearing nocturnal, white zygomorphic flowers. Floral bracts in this taxon exceed the pedicels in length. On the occasions when I have collected *V. umbrosa* in flower, the flowers have had a sweet, pleasant fragrance in the early evening and have produced copious nectar. Although confirmatory observations are lacking, this odor, combined with nocturnal anthesis, suggest a night flying insect pollinator.

Vriesea umbrosa is most closely related to *V. greenbergii* and their relationship and the features which distinguish them are discussed under the latter species.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: west on the road from Zapote to Santa Elena or about 7-10 km north-northwest of Zarcero, 16 April 1976 *Utley & Utley 4656* (CR), *4657* (US), *4658* (DUKE), *4659*(NOLS), *4660* (GH), *4671* (MO), *4672* (F), *4673* (NY). CARTAGO PROVINCE: about 8 km north of El Empalme near the road to Palmital, 6 April 1974, *Utley & Utley 814* (DUKE); on the road from Tapantí to Taus and Tausito about 3 km northeast of the Río Grande de Orosí at Tapantí, 27 May 1976, *Utley & Utley 5019* (DUKE). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: about 1 km north of the road to San Cristóbal Norte on the Interamerican Highway, 9 May 1976, *Utley & Utley 4753* (DUKE). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: about 5 km northeast of San Isidro de Heredia on Calle Yerbabuena, 3 April 1976, *Utley & Utley 4478* (DUKE) & *4480* (F). SAN JOSÉ PROVINCE: between San Jerónimo and Alto de La Palma on Hwy. 220, 19 June 1975, *Utley & Utley 2570* (DUKE) & *2571* (CAS); between Bajo La Hondura and Alto de La Palma, 24 May 1976, *Utley & Utley 5004* (NOLS) & *5005* (DUKE). PANAMÁ: PROVINCE OF PANAMA: road to Altos de Pacora, near schoolhouse, 8 October 1974, *Mori & Kallunki 2344* (MO).

7. *Vriesea latissima* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

> *Thecophyllum latissimum* Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 1122. 1904.
> TYPE: COSTA RICA: without further location, *Werckle 82* (HOLOTYPE: B!, photograph US!).

> *Vriesea rainfera* L. B. Smith, Phytologia 9: 242. 1963. TYPE: COSTA RICA: SAN JOSÉ PROVINCE: in cloud forests of El Alto de la Palma, *C.K. Horich s.n.;* University of California Botanical Gardens accession number 58.482-1 (HOLOTYPE: US!).

Epiphytic acaulescent. LEAVES in a spreading rosette, 45.0-67.0 cm long; *blades* 23.0-35.0 (40.0) cm long and 9.0-11.0 cm wide, green adaxially, strongly suffused with maroon abaxially, ligulate, apex rounded and acuminate; *sheaths* 24.0-28.0 cm long and 11.0-12.0 cm wide, scarcely wider than the blades, pale brown becoming green suffused with maroon distally, broadly elliptic. SCAPE erect 60.0-67.0 cm long and about 1.0 cm in diameter; *bracts* 6.0-7.0 cm long and 4.0-5.0 cm wide, exceeding the inter-

nodes, green to green strongly suffused with maroon, erect. INFLORESCENCE erect, 32.0-52.0 cm long and 9.0-10.0 cm in diameter, axis green or green deeply suffused with maroon; *primary bracts* 5.0-6.0 cm long and 3.0-5.0 cm wide, green frequently mottled with maroon to entirely purple or brown-maroon, divergent to subspreading, apex acute to rounded and acuminate. LATERAL BRANCHES divergent to spreading, 3.5-6.0 cm long, distichously 4-to 5-flowered, occasionally subsecund at anthesis, peduncle 1.0-2.0 cm long, rachis 2.0-3.7 cm long. FLOWERS 0.1-0.5 cm pedicellate; *floral bracts* 2.0-3.0 cm long and 1.0-3.0 cm wide, slightly shorter than to about equalling the sepals, green to green spotted or suffused with purple, subcoriaceous, ovate to elliptic, apex acute; *sepals* 2.1-2.8 cm long and 1.1-1.3 cm wide, green, frequently suffused with maroon proximally, coriaceous, elliptic, apex broadly acute or obtuse to rounded; *petals* about 3.5 cm long and 1.5 cm wide, white, obovate; *appendages* 0.4 cm long and 0.1-0.2 cm wide; *stamens* in a hood configuration over gynoecium, anthers laterally connivent, filaments 2.2-2.3 cm long, anthers 0.7 cm long; *ovary* 0.5 cm long and 0.4 cm in diameter, style 2.5 cm long.

PHENOLOGY: Flowering specimens have been collected in April.

DISTRIBUTION AND HABITAT: Known only from Costa Rica in the region between 900-1500 m in the premontane rain forest life zone.

DISCUSSION: The conspicuous features which set *Vriesea latissima* apart from most other thecophylloid vrieseas include a spreading rosette, broad (9.0-11.0 cm), ligulate leaves that are green adaxially but maroon abaxially, a stout scape and coriaceous floral bracts which are 2.0-3.0 cm long. Unlike other members of the pedicellata complex, lateral branches of the inflorescence of *V. latissima* are coated with a gelatinous exudate. This condition had been noted in several groups in the hygrometrica complex, the comata, capitata and hygrometrica species groups.

The white nocturnal flowers of *V. latissima* become subsecund at anthesis. The observed floral syndrome of these large white, nocturnal flowers, borne on a stout inflorescence well above the surrounding foliage, is compatible with that presented by Faegri and van der Pijl (1971) for chiropterophilous plants. In fact, bats have been observed visiting the flowers of *V. latissima* (Phillip De Vries, pers. comm.).

Vriesea latissima shares a number of characters with *V. greenbergii* and *V. umbrosa.* In all three species the lateral branches of the inflorescence are short, stout pedunculate, with well-developed rachises. Their short pedicellate flowers are subtended by coriaceous floral bracts which exceed the pedicels in length. *V. latissima* is easily separated from *V. greenbergii* and *V. umbrosa* on the basis of leaf width, floral bract length and floral morphology.

In the vegetative condition, *V. latissima* may be mistaken for *V. leptopoda* since they share a common leaf and rosette morphology. However, these taxa are not sympatric and have different elevational distributions. *V. latissima* is consistently found between 900 m and 1500 m in elevation; in contrast, *V. leptopoda* grows at higher elevations (1600-2300 m). In flower or fruit *V. latissima* may be distinguished from *V. leptopoda* by pedicel, sepal and floral bract length.

Vriesea ranifera was characterized by Smith (1963) and Smith and Downs (1977) as having scape bracts which equaled or exceeded the internodes; in contrast, scape bracts of *V. latissima* appeared to be shorter than the internodes. While the scape bracts of the type specimen of *V. latissima* are, in fact, shorter than the internodes, this is a result of the age of the inflorescence, which is well past fruiting, and is also a consequence of the drying and weathering of the scape

bracts, which are largely wanting. This condition, though not readily observable in a photograph of the type of *V. latissima*, is obvious upon critical examination of the type material. The type of *V. ranifera* agrees well with that of *V. latissima* in numerous characters, including rosette shape, leaf shape, width and color pattern, lateral inflorescence development, peduncle length, and sepal length and width. In the absence of demonstrable differences in critical characters and in view of a compelling series of common characters, *V. ranifera* must be considered a synonym of *V. latissima*.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: fields, road banks and forest remnants between Los Angeles Norte and ca 7 km north of La Balsa de San Ramón or about 10-17 km north of San Ramon, 8 August 1975, *Utley & Utley 2814* (DUKE) & *2884* (CR). BORDER OF HEREDIA AND SAN JOSE PROVINCES: 5 km northeast of San Isidro de Heredia on Calle Yerbabuena, 3 April 1976. *Utley & Utley 4470* (DUKE) & *4479* (NOLS). SAN JOSE PROVINCE: La Palma, *Werckle 12* (US); between La Hondura and Alto de La Palma, 24 May 1976, *Utley & Utley 5006* (DUKE).

8. *Vriesea lyman-smithii* Utley, sp. nov.

Fig. 19

A *V. nephrolepis* L.B. Smith & Pitt. cui valde affinis corollis subtubularibus, sepalis rotundis, stylis brevioribus, capsulis longioribus differt.

Epiphytic, acaulescent. LEAVES in a spreading to subspreading rosette, 45.0-61.0 cm long; *blades* 25.0-35.0 cm long and 4.2-7.0 cm wide, green to green suffused with purple, ligulate to broadly triangular, acute; *sheaths* 20.0-26.0 cm long and (7.5) 9.5-11.5 cm wide, pale brown at times with an abaxial, basal castaneous band, usually with maroon wavy crossbands in the distal region, ovate to elliptic. SCAPE erect (45.0) 55.0-68.0 cm long and 0.7-1.0 cm in diameter; *bracts* 7.0-15.0 cm long, blades 3.5-9.0 cm long and 1.8-4.0 cm wide, green or green with a fine maroon margin and apex, drying to brown, erect to spreading or divergent, occasionally spirally involute, triangular, acute; *sheaths* (3.2) 3.6-5.2 (5.8) cm long and 4.0-6.6 cm wide, drying ochre abaxially and light brown adaxially, sheathing-erect ovate. INFLORESCENCE erect, 16.0-33.0 cm long and 9.0-14.0 cm in diameter, cylindric to conical in outline, surface glabrous; *primary bracts* 7.0-13.2 cm long, *blades* (3.0) 3.6-5.2 (7.8) cm long and 2.0-3.0 cm wide, green, divergent to spreading frequently reflexed at or near the junction with the sheath, triangular with an acute apex, sheath 3.5-5.7 cm long and 4.2-6.7 cm wide, drying ochre abaxially, pale brown adaxially, ovate. LATERAL BRANCHES spreading, 0.4-1.0 cm long, bearing 2 collateral or subcollateral flowers, occasionally with a vestigial third flower, peduncles 0.4-1.0 cm long, rachis 0.0-0.3 cm long. FLOWERS sessile or to 0.3 cm pedicellate; *floral bracts* 0.9-1.4 cm long and 1.6-2.3 cm wide, membranaceous to subcoriaceous, finely nerved, usually brown to pellucid punctate abaxially and obscurely lepidote adaxially, broadly ovate to reniform, apex obtuse to broadly rounded, frequently minutely acuminate or torn-incised; *sepals* 2.0-2.6 cm long and 1.6-2.1 cm wide, green with maroon margins, drying brown, coriaceous, occasionally keeled, glabrous abacially, lepidote adaxially, elliptic to obovate, apex obtuse to rounded or broadly rounded; frequently suffused with maroon proximally, coriaceous, elliptic, apex broadly acute or obtuse to rounded; *petals* 3.6-4.0 cm long and 1.7-1.9 cm wide, white to greenish white, ovate to elliptic, incised on either side where the petals are exserted from the sepals; *appendages* 0.7-0.8 cm long and 0.3-0.5 cm wide, *stamens* in a hood configuration over the stigma, filaments 2.2-2.9 cm long, anth-

ers 0.9-1.1 cm long; *ovary* 0.8-1.0 cm long and 0.5-0.6 cm in diameter, style 1.7-2.1 cm long; *capsule* 4.9-5.3 cm long and 1.3-1.5 cm in diameter, castaneous, obovate.

TYPE: COSTA RICA: HEREDIA PROVINCE: 1-2 km south of the junction of highways 9 and 120 on Hwy. 9, slopes above the Río Desengano, 22 May 1976, *Utley & Utley 4960* (HOLOTYPE: DUKE!; ISOTYPES: CAS!, CR!, DUKE!, F!, MO!, US!).

PHENOLOGY: Flowering specimens have been collected in May and June.

DISTRIBUTION AND HABITAT: Known from the Cordillera Central de Costa Rica and the northern slopes of the Cordillera de Talamanca between 1500-2100 m in the lower montane rain forest life zone.

DISCUSSION: *Vriesea lyman-smithii* is recognizable at once by its relatively broad leaves which form a spreading rosette, its stout scape and dense inflorescence. The sheaths of the primary bracts are broad and tend to cover the relatively large sepals. Flowers of *V. lyman-smithii* are white to greenish white and nocturnal. The corollas are subtubular with the two adaxial petals arranged in a position to form a normal tubular corolla; however,the abaxial petal is flexed slightly outward.

Vriesea lyman-smithii is most closely allied with *V. nephrolepis* from which it differs by a combination of characters. The scape is generally longer than that of *V. nephrolepis*, while the sheaths of the primary bracts are broader than those of *V. nephrolepis*. The broad primary bract sheaths in conjunction with a more dense nature of the inflorescence give the inflorescence of *Vriesea lyman-smithii* a characteristic appearance in both living plants and dried herbarium material. These features, when taken together with the subtubular flowers, generally rotund sepals and shorter styles (1.7-2.1 cm vs. 2.4-3.7 cm) and larger capsules (4.9-5.3 cm vs. 2.4-3.7 cm), consistently separate *Vriesea lyman-smithii* from *V. nephrolepis*.

Despite the rather recondite nature of some of the characters, the two species are readily separable in the field as well as in the herbarium. Although both taxa occur in the lower montane rain forests, they are generally allopatric. However, they have been encountered growing sympatrically at Cerro Zurqui in the Cordillera Central.

ETYMOLOGY: This species is named in honor of Dr. Lyman B. Smith of the Smithsonian Institution whose monumental labors in the taxonomy of the Bromeliaceae have stimulated and formed the basis for studies of the biology, ecology and systematics of this unique epipthytic family. Dr. Smith has willingly shared his vast knowledge and experience with all who have sought his advice.

SPECIMENS EXAMINED: COSTA RICA: HEREDIA PROVINCE: region north of Cerro Chompipe, about 15 km northeast of Heredia and 3 km north of Cerro Redondo de La Cruz, 15 October 1974, *Utley & Utley 1313* (DUKE); 8 December 1975, *Utley & Utley 3583* (DUKE). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: along the Río Para Blanco in the vicinity of Cerro Zurquí, 18 June 1974, *Utley & Utley 963* (DUKE). SAN JOSÉ PROVINCE: 4 km north of Cascajal or 7 km north of Las Nubes on Hwy. 216, 3 July 1976, *Utley & Utley 5271* (DUKE).

9. *Vriesea nephrolepis* L.B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953 Figs. 14, 20.
Thecophyllum werckleanum Mez, Bull. Herb. Boiss. ser. II. 3: 139. 1903 not *Vriesea werckleana* Mez, 1903.
TYPE: COSTA RICA: near Cartago, elev. 1200-1400 m, *Werckle in Herb. Inst. Phys.-Geogr. Costar.* 16201 (HOLOTYPE: B!; ISOTYPES: B! GH).

Thecophyllum montanum L.B. Smith in Yuncker, Field Mus. Bot. 17: 319. 1982.

TYPE: HONDURAS: COMAYAGUA: El Achote summit , above Siguatepeque, *Yuncker, Dawson & Youse 6423*. (HOLOTYPE: GH!).

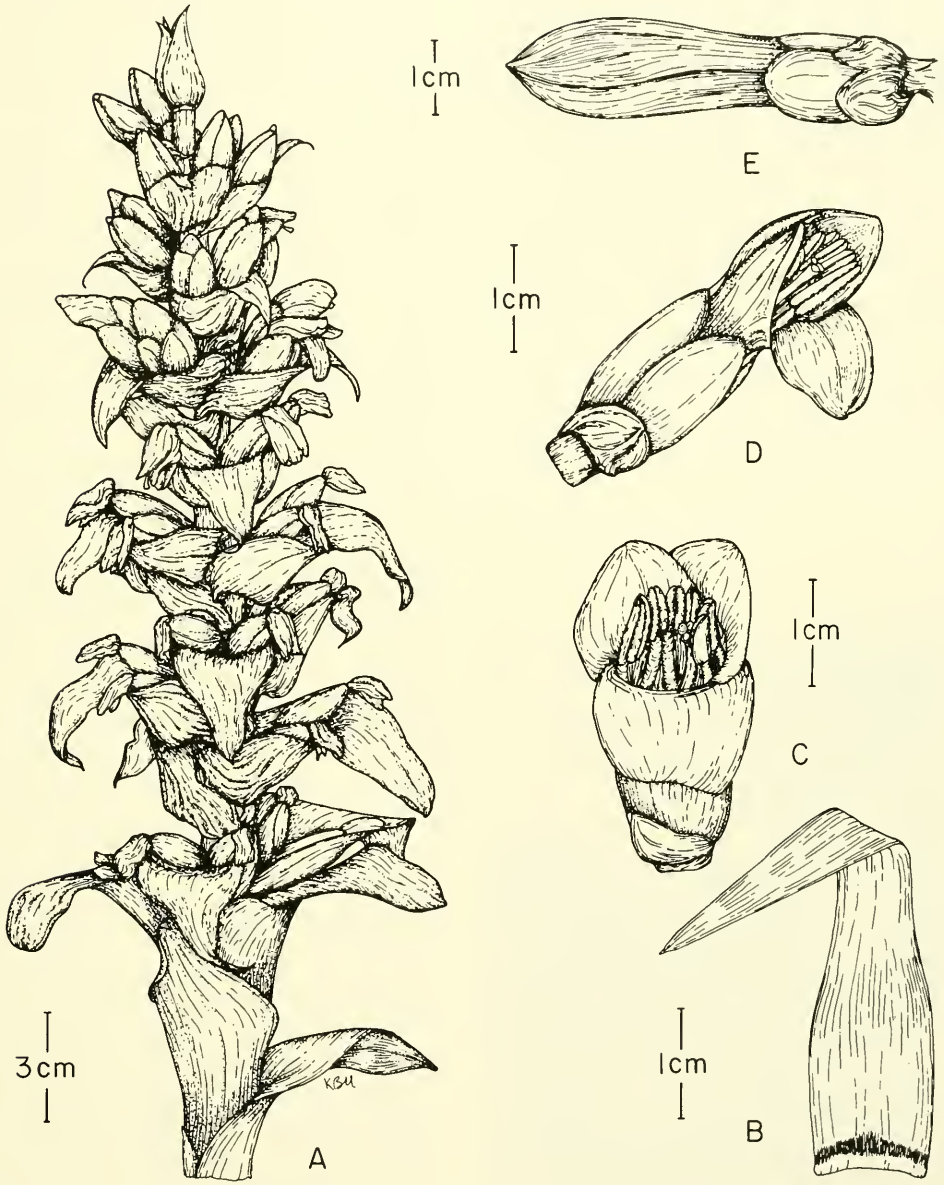


Fig. 19 *Vriesea lyman-smithii*. A. Inflorescence; B. Leaf; C & D. Flower with floral bract; E. Mature capsule with sepals and floral bract. A, B, from *(Utley & Utley 4960)*; C & D from *(Utley & Utley 4981)*; E, from *(Utley & Utley 1313)*.

Vriesea montana (L.B. Smith) L.B. Smith & Pitt. J. Wash. Acad. Sci. 43: 69. 1953.

Epiphytic or rarely terrestrial, acaulescent to 15 cm caulescent. LEAVES in a spreading rosette, (20.0) 27-46 (61.0) cm long; *blades* (9.0) 13-35 (42.0) cm long and 3.4-6.2 cm wide, green or at times suffused with maroon, usually with dark green wavy crossbands, these frequently suffused with maroon near the blade-sheath junction or occasionally suffused with maroon throughout the blade, ligulate, apex acute to acuminate or rounded and acuminate or rarely attenuate; *sheaths* 10.0-22.0 (26.0) cm long and (5.2) 6.2-9.6 (10.4) cm wide, pale brown, frequently with a basal castaneous band or medial castaneous spot on the abaxial surface or rarely the entire abaxial surface castaneous, elliptic to ovate or rarely obovate, usually with fine maroon wavy crossbands in the upper portion. SCAPE erect or curved-erect, 27.0-57.0 (67.0) cm long and (0.3) 0.4-0.7 (1.0) cm in diameter; *bracts* erect to erect and spreading distally, reflexed or rarely spirally involute distally, (3.6) 5.0-12.0 (16.2) cm long, blades (1.6) 2.0-8.6 (11.1) cm long and 0.9-3.3 (4.5) cm wide, green with green, maroon or pinkish transverse lines, the upper usually dried brown at anthesis, triangular to subligulate with an acute apex, sheaths clasping erect, (1.6) 2.0-4.4 (5.8) cm long and (2.2) 2.8-5.0 (5.6) cm wide, ochre to green in living material, drying to ochre or brown to castaneous abaxially and pale brown adaxially, ovate to elliptic. INFLORESCENCE erect, 9.0-28.0 (32.0) cm long and 4.0-10.0 (12.0) cm in diameter, cylindric, rachis glabrous; *primary bracts* spreading to subascending, usually reflexed or occasionally spirally involute at the blade sheath junction (3.2) 4.0-8.6 (10.8) cm long, *blades* 1.6-5.6 (7.1) cm long and 0.8-3.2 cm wide, green, at times tinged with maroon near margins, frequently with dark green or pink to red wavy crossbands, usually drying to brown at anthesis, triangular in shape with an acute or rarely acuminate apex; sheath 1.6-4.2 cm long and (2.2) 2.8-5.4 cm wide, green or green with a trace of ochre to strongly ochre in living material, drying brown to ochre abaxially and pale brown to white adaxially, ovate to rarely elliptic. LATERAL BRANCHES spreading, 2flowered, occasionally with a third vestigial bud, sessile to 0.6 (1.0) cm pedunculate, rachis usually wanting and the flowers collateral, or to 0.3 cm long and the flowers subcollateral. FLOWERS sessile to 0.6 (0.8) cm pedicellate; *floral bracts* 0.8-1.4 cm long and (1.1) 1.3-2.0 (2.2) cm wide, subcoriaceous or rarely coriaceous, pale green or green, at times suffused with maroon, drying brown, glabrous or minutely brown to pellucid punctulate abaxially and scattered lepidote adaxially, suborbicular, broadly ovate to ovate or reniform, apex truncate to obtuse or

Fig. 20. *Vriesea nephrolepis*, habit.

broadly rounded, at times minutely acuminate, frequently tearing medially and appearing incised, keel usually wanting, occasionally present and inflated; *sepals* 1.5-2.2 (2.6) cm long and 1.0-2.0 cm wide, coriaceous, green frequently suffused with maroon especially marginally or apically drying brown to castaneous, elliptic to obovate, apex rounded to broadly rounded or obtuse; *petals* (3.1) 3.4-4.5 (5.4) cm long and 1.2-1.9 cm wide, white to greenish white, ovate-lanceolate to lanceolate or slightly obovate, constricted at the point where the petals emerge from the sepals; *appendages* 0.3-0.8 cm long and 0.2-0.4 cm wide, *stamens* in a hood over the gynoecium, usually connivent by the lateral margins of the anthers into a single grouping of six or two groupings of three, rarely free, filaments (2.5) 2.9-3.9 (4.7) cm long, anthers 0.6-1.0 cm long; *ovary* 0.6-0.8 cm long and 0.4-0.5 cm in diameter, style 2.4-3.7 (5.0) cm long; *capsule* 3.3-4.3 cm long and 1.1-1.7 cm in diameter, castaneous, fusiform to obovate.

PHENOLOGY: Flowering specimens have been collected in March through July with a distinct peak occurring March-May.

DISTRIBUTION AND HABITAT: Known from Costa Rica and Panama northward to Guatemala between 1500-2800 m in the lower montane wet forest and rain forest life zones and the premontane and montane rain forest life zones.

DISCUSSION: *Vriesea nephrolepis* is the most commonly encountered night flowering taxon in the Cordillera de Talamanca and the volcanos of the Cordillera Central in Costa Rica. It is a distinctive species characterized by a spreading rosette form and green leaves which are frequently suffused with maroon and green to maroon wavy transverse lines. The inflorescence of *V. nephrolepis* is erect and basally lax, bearing large white to green-white nocturnal flowers with zygomorphic corollas. The primary bracts are generally green, or rarely green with maroon wavy transverse lines at anthesis. Specimens have also been collected in which the primary bracts are either dried and brown at anthesis or very infrequently green suffused with red-maroon at anthesis. The primary bract sheaths of *V. nephrolepis* are frequently ochre colored and become rugose upon drying.

Although the type of *V. nephrolepis* lacks corollas, the rugose sheaths of the primary bracts are prominent. The dense aggreated wavy crossbands which are present in the leaves of many collections are also characteristic of the type material of *V. nephrolepis*. The type collection of this taxon was made in the vicinity of Cartago between 1200 and 1400 m. This is more than 500 meters below the lowest elevation at which I have collected *V. ororiensis*, but within 100 m of the lowest collections of *V. nephrolepis* . Collections from the lower slopes of the Cordillera de Talamanca near Cartago agree in general size, leaf markings, vigor and form of the inflorescence and the form of the primary bracts and sepals with the type collection. This correlation of elevation, general locality and critical morphological features support the interpretation of *V. nephrolepis* that I employ.

Although Smith (1977) stated that *V. nephrolepis* was only known from the type material, there were a number of collections of this taxon available but they were identified as *V. irazuensis*, a taxon which is conspecific with *V. ororiensis*. This is presented in greater detail in the discussion of *V. ororiensis*. Both Mez (1934-1935) and Smith (1977) emphasized the number of flowers in the lowermost branches of the inflorescences. In Mez's treatment *V. nephrolepis* (*Thecophyllum werckleanum*) keys out only under the lead that requires three flowers per lateral branch. Smith's monograph is similar in this respect. While the type of *V. nephrolepis* does have three flowers in the lowermost lateral branches, this is an unusual condition. The most frequent number of flowers per lateral branch that I observed in my

collections was two. Smith (1938) established *Thecophyllum montanum* (*Vriesea montana*) and distinguished the new taxon from *Thecophyllum werckleanum* on the basis of sheath color, size and density of primary bracts and shape of the floral bracts. The type and other specimens of *V. montana* I have seen fall well within the range of variation observed in *Vriesea nephrolepis* and I consider the two taxa to be conspecific. The solution to the problems associated with *V. ororiensis, V. nephrolepis* and *V. montana* was dependent on extensive field work. The collections extant at the time of Mez's and Smith's treatments were insufficient to address these problems.

Vriesea nephrolepis is similar to *V. lymansmithii* and their relationship is elaborated in the discussion of the latter species. In the vegetative or fruiting condition, *V. nephrolepis* is easily confused with *V. ororiensis*. The best character for separating these morphologically very similar taxa in fruit is the marked tendency for the primary bracts of *V. nephrolepis* to appear rugose in sheath area upon drying. In flower the floral syndromes of these taxa are distinctly different and permit unequivocal identification of both *V. ororiensis* and *V. nephrolepis*.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: between the junction of highways 9 and 120 and the summit of Volcán Poas, 11 March 1975, *Utley & Utley 1927* (DUKE) & *1928* (CR); on the finca of Mike Canon near the junction of highways 9 and 120, 20 July 1975, *Utley & Utley 2664* (DUKE); between Poasito and Volcán Poas, along Hwy. 120. CARTAGO PROVINCE: 6 miles south of Cartago on Interamerican Highway, Talamanca Mountains, 10 July 1962, *Haines & Haines 676* (US); 10 miles south of Cartago on Interamerican Highway, Talamanca Mountains, 10 July 1962, *Haines & Haines 685* (US); 19 miles south of Cartago on Interamerican Highway, Talamanca mountains, 10 July 1962, *Haines & Haines 700* (US); 16 miles south of Cartago on Interamerican Highway, north slope of Talamanca Mountains, 17 July 1962, *Haines & Haines 722* (US); 21 miles south of Cartago on the Interamerican Highway, north slope of Talamanca Mountains, 19 July 1962, *Haines & Haines 730* (US); Estate of C.H. Lankester, 27 February 1966, *L.B. Smith 15301* (US); on tree, cloud forest, Aserrí, 19 March 1966, *L.B. Smith 15325* (US) & *15326* (US); Cerro de La Carpintera, February 1924, *Standley 34463* (US); south of Cartago, about 3 km south of the Interamerican Highway on a secondary road, vicinity of Palo Verde, 17 April 1975, *Utley & Utley 2190* (NOLS), *2191* (DUKE) & *2192* (UC); 3-6 miles south of San Isidro de Cartago on the Interamerican Highway; 8 June 1975, *Utley & Utley 2518* (DUKE) & *2537* (US); about 1/2 km south of Pacayas on Hwy. 230, 25 July 1975 *Utley & Utley 2708* (DUKE), *2709* (F) & *2710* (DUKE); on Hwy. 230 between Trinidad and Coliblanco, 25 July 1975, *Utley & Utley 2711* (DUKE), *2720* (MO) & *2721* (NOLS); on Hwy. 216 beyond Cascajal, northwestern slopes of Volcán Irazu, 10 December 1975, *Utley & Utley 3617* (DUKE); BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: in the vicinity of a montane bog 17 km southeast of El Empalme on the Interamerican Highway, 6 April 1974, *Utley & Utley 809* (DUKE); within 2-3 km of the Interamerican Highway on the road from El Empalme to Santa María de Dota, 6 April 1974, *Utley & Utley 816* (DUKE); junction of highways 2 and 223 about 5 km north of El Empalme, 16 April 1975, *Utley & Utley 2169* (DUKE); Interamerican Highway about 12 km southeast of El Empalme in the vicinity of Paso Macho, 3 August 1975, *Utley & Utley 2745* (DUKE), *2749* (CR) & *2750* (DUKE). HEREDIA PROVINCE: roadside and tree falls between Vara Blanca and Chinchona on Highway 9, 16 October 1974, *Utley & Utley 1320* (DUKE), *1321* (US) & *1322* (F); upper slopes of Volcán Barba about 8 km beyond Porosatí, 16 March 1975, *Utley &*

Utley 1964 (DUKE); 12 April 1975 *Utley & Utley 2040* (DUKE), *2046* (GH), *2047* (NY), *2048* (CAS) & *2049* (NOLS); about 1 km south of Monte de la Cruz on Hwy. 113, 1 April 1976, *Utley & Utley 4448* (DUKE); 2 km south of the entrance to Parque Nacional Volcán Poas, 3 May 1976, *Utley & Utley 4711* (DUKE), *4713* (NOLS), *4714* (F), *4715* (GH), *4716* (B), *4717* (MO), *4718* (K), *4719* (NY), *4720* (BM), *4721* (DUKE), *4722* (MICH), *4723* (CR), *4724* (NOLS), & *4725* (DUKE); near the junction of highways 9 and 120, 21 June 1976, *Utley & Utley 5153* (DUKE) & *5156* (NOLS). BORDER OF-HEREDIA AND SAN JOSE PROVINCE: along the Río Para Blanco near Cerro Zurquí, 10 July 1974, *Utley & Utley 935* (DUKE); 18 June 1974, *Utley & Utley 973* (DUKE); 22 December 1974, *Utley & Utley 1748* (DUKE). SAN JOSÉ PROVINCE: between San Jerónimo and Alto de La Palma on Hwy. 220, 1 June 1974, *Utley & Utley 892* (DUKE); between San Jeronimo and Alto de La Palma on Hwy. 220, 29 June 1974, *Utley & Utley 991* (DUKE); 1-2 km south of the Interamerican Highway on the road from El Empalme to Santa María de Dota, 16 April 1975, *Utley & Utley 2159* (MO), *2161* (F), *2164* (DUKE) & *2168* (MO); between San Jerónimo and Alto de La Palma on Hwy 220, 1 June 1974, *Utley & Utley 892* (DUKE); between San Jerónimo and Alto de La Palma on Hwy. 220, 6 July 1975, *Utley & Utley 2584* (F), *2585* (US), *2591* (DUKE) & *2596* (US); between Cascajal and 8 km northeast on Hwy. 216, 23 August 1975, *Utley & Utley 2944* (DUKE); Cedral (Cerros de Escazú), approach to and summit of Cerro Daser about 3-5 km southwest of Aserrí, 13 March 1976, *Utley & Utley 4264* (DUKE), *4266* (DUKE), *4282* (CR) & *4286* (MICH); 2 April 1976, *Utley & Utley 4450* (CAS) & *4451* (DUKE); at Cascajal about 3 km north of Las Nubes on Hwy. 216, 3 July 1976, *Utley & Utley 5239* (DUKE), *5240* (US), *5252* (CR) & *5253* (F). EL SALVADOR: DEPARTMENT OF SANTA ANA: moist cloud forest on Cordillera Miramundo, Mountain of Montecristo, 27-31 January 1966, *Molina, A. W. Burger and B. Wallenta 16920* (US). HONDURAS: Montana Uyuca, off Tegucigalpa-Zamorano road, trail starts Km. 25, 10 July 1964, *Gilmartin, A.S. 956* (US). PANAMA: PROVINCE OF VERAGUAS: NW of Santa Fe, 8.8 km from Escuela Agricola Alto de Piedra. Pacific Slope, 25 February 1975, *Mori & Kallunki 4845* (MO).

10. *Vriesea ororiensis* (Mez) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953.

Figs. 11, 16

Guzmani ororiensis Mez in DC. Mon. Phan. 9: 917. 1896.

TYPE: COSTA RICA: Province not given, *Oersted Brom. n. 25,* Volcán Irazu, elev. 2200 m; *Donnell Smith 4963.* [LECTOTYPE: *Oersted Brom. n. 25* (C!); SYNTYPE: *Donnell Smith n. 4963* (US!)].

Thecophyllum ororiense (Mez) Mez, Bull. Herb. Boiss. ser. II. 3: 131. 1903.

Thecophyllum crassiflorum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II 3: 138. 1903.

TYPE: COSTA RICA: Province not given, near Cartago, elev. 1200-1400 m, *Werckle, Inst. Phys-Geogr. Costar. 16188*

Thecophyllum irazuense Mez & Werckle, Bull. Herb. Boiss. ser. II. 3: 138. 1903.

TYPE: COSTA RICA: Province not given, on Volcán Irazu near Las Pacayas de Cartago, elev. 1800 m, *Werckle, Inst. Phys. -Geogr. Costar. 16206.* (HOLOTYPE: B!, photograph US!; ISOTYPE: GH).

Thecophyllum standleyi L.B. Smith, Contr. Gray Herb. 117: 30. 1937.

TYPE: COSTA RICA: SAN JOSÉ: on tree in páramo thicket, Cerro de las Vueltas, elev. 2700-3000 m, *Standley & Valerio 43573* (HOLOTYPE: US!).

Thecophyllum cylindraceum Suessenguth & Goeppinger, Bot. Jahrb. 72: 292. 1942.
TYPE: COSTA RICA: Canaan, elev. 1300 m, *Kupper 1252* (HOLOTYPE: M!, photograph US!).

Thecophyllum kupperi Suessenguth & Goeppinger, Bot. Jahrb. 72: 292. 1942.
TYPE: COSTA RICA: Location not given, *Kupper s.n.* (HOLOTYPE: M!, photograph US!).

Vriesea crassiflora (Mez & Werckle) L.B Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

Vriesea irazuensis (Mez & Werckle) L.B Smith & Pitt. J Wash. Acad. Sci. 43: 403. 1953.

Vriesea standleyi (L.B. Smith) L.B Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953.

Vriesea cylindraceae (Suessenguth & Goeppinger) L.B Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

Vriesea kupperi (Suessenguth & Goeppinger) L.B Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

Epiphytic or rarely terrestrial, acaulescent to short (4.0-6.0 cm) caulescent. LEAVES 17.0-48.0 cm long; *blades* 13.5-36.0 (46.5) cm long and (2.7) 3.3-6.5 (7.3) cm wide, green or green variously suffused with maroon, occasionally entirely maroon, usually with fine wavy cross bands, these maroon, dark green or dark green suffused with maroon, commonly more distinct abaxially or near the blade-sheath junction, ligulate to subligulate or rarely broadly triangular, apex acute or acuminate to attentuate or rounded and acuminate; *sheaths* (7.5) 10.0-25.0 cm long and 5.0-10.5 cm wide, castaneous abaxially and pale brown adaxially or pale brown on both surfaces, usually with castaneous band near base and with dark green or maroon wavy cross bands distally, elliptic to obovate. SCAPE erect or curved-erect, (32.0) 35.0-68.0 (74.0) cm long and 0.3-1.0 cm in diameter; *bracts* 2.4-24.5 cm long; blades 1.8-14.0 (19.0) cm long and (1.0) 1.6-3.4 (4.2) cm wide, blades of the lowermost bracts usually green with dark green, maroon or red wavy cross-bands, middle and upper green, pale cream, pink or crimson with cross-bands of pink to crimson, erect to divergent distally, ligulate to subligulate, apex rounded or attentuate rarely rounded and short acuminate, sheaths 0.6-5.0 cm long and 2.2-4.5 (5.5) cm wide, ochre or green occasionally suffused with red or pink, drying ochre to pale brown abaxially and pale brown adaxially, if colored when living occasionally retaining a trace of the color when dry, clasping-erect, ovate to elliptic. INFLORESCENCE erect, (8.0) 19.0-35.0 (39.0) cm long and 5.0-12.0 cm in diameter, cylindric to subcylindric or narrowly conical in outline, rachis glabrous green to green mottled with maroon or scarlet or entirely scarlet; *primary bracts* spreading at anthesis, frequently drooping-reflexed or spirally recurved at the blade-sheath junction, blades 1.8-9.5 (13.9) cm long and 1.1-4.0 cm wide, pink to scarlet, frequently with fine, wavy pink to crimson cross bands, triangular to subligulate or rarely ligulate, apex acute to rarely acuminate or attenuate, sheaths (1.1) 1.6-3.8 (4.4) cm long and (2.2) 2.4-4.5 (6.0) cm wide, green to pale cream or ochre occasionally suffused with pink to red wavy cross-bands, ovate to elliptic. LATERAL-BRANCHES spreading, to subascending, 2-flowered or rarely with a third vestigial bud, sessile to 1.1 cm pedunculate, rachis absent and the flowers collateral to 0.3 (0.6) cm long and the flowers subcollateral. FLOWERS sessile to 0.5 cm pedicellate,

floral bracts 0.7-1.7 cm long and 1.0-1.2 cm wide, subcoriaceous to membranaceous, keel usually pronounced, frequently inflated, rarely obscure to wanting, green to pale green occasionally weakly suffused with red or maroon, drying brown post anthesis, abaxial surface minutely pitted, usually with castaneous to pellucid punctulae, finely nerved or rarely subeven, scattered lepidote adaxially, ovate or broadly ovate to elliptic or suborbicular, apex acute to obtuse or acuminate or rounded and minutely acuminate, at times rostrate, frequently torn at anthesis and the shape not obvious; *sepals* (1.3) 1.5-2.4 cm long and 1.1-2.0 cm wide, coriaceous, keeled, green drying yellow-green or castaneous, obovate to elliptic, apex round, torn-incised to truncate or acute; *petals* (2.0) 2.5-3.0 (3.4) cm long and 0.8-1.3 cm wide, green elliptic to obovate or subpandurate; *appendages* (0.2) 0.6-0.7 cm long and 0.1-0.3 cm wide, *stamens* in a hood configuration over the gynoecium, filaments (1.2) 1.4-2.0 cm long, anthers 0.6-0.9 cm long, coherent laterally into an androecial hood; *ovary* 0.4-0.6 cm long and 0.3-0.4 cm in diameter, style (1.4) 1.6-1.9 cm long frequently flexed abaxially and the stigma oriented away from the androecial hood; *capsule* about 2.9 cm long and 1.0 cm in diameter, fusiform.

PHENOLOGY: Flowering January through April with a distinct peak in March and April.

DISTRIBUTION AND HABITAT: Known from the Cordillera Central and Cordillera de Talamanca in Costa Rica and the Chiriquí region of Panamá.

DISCUSSION: Although *Vriesea ororiensis* was better represented in herbaria than any other thecophylloid vriesea, the specimens available were not sufficient to permit a thorough evaluation of the species. Intensive collecting of *V. ororiensis* in Costa Rica has resulted in a much broader concept of this species than previously existed. *Vriesea ororiensis* is one of the most abundant and conspicuous thecophylloid vrieseas in Costa Rica, being the dominant *Vriesea* in montane regions.

Vriesea ororiensis is an extremely variable taxon in general robustness as well as in the size, color, and markings of the primary bracts. Within a single large population on Volcán Barba, the primary bracts vary in length from 3.1 cm to 11.4 cm and their color varies from pink with dark red wavy transverse lines to totally crimson. There seems to be a correlation between elongate primary bracts and pink color with wavy transverse lines and, conversely, between short primary bracts with deep crimson coloration. Moreover, plants with elongate primary bracts are generally larger, with elongate scapes and inflorescences, whereas the forms with short crimson primary bracts tend to be more compact with shorter scapes and inflorescences. This initially appeared to be correlated with exposure to sunlight; however, field observations revealed the two extremes growing side by side in both exposed locations and deep shade. This range in variation is reflected in most other populations that I sampled (Volcán Poas, Volcán Irazu, Cerro Dasser) but the Barba population is the most variable. Collections from the Cordillera de Talamanca exhibit greater robustness and longer primary bracts than those from other areas. In contrast to this variability in color and size of the scape and primary bracts the flowers are consistently greenish with tubular corollas and diurnal anthesis. This extreme variation in a small suite of characters has resulted in several populational or geographical variants previously being recognized as distinct species.

Examination of the type material and the correlation of the specimens with my field observations show that Mez misinterpreted the inflorescence orientation of *V. ororiensis*. The inflorescence of this species is erect at anthesis, and not pendent as he stated in

Monographiae Phanerogamarum (1896) and Das Pflanzenreich (1934-1935). Smith and Downs (1977) also state that the inflorescences of *V. ororiensis* are pendent. In the case of *V. balanophora,* I believe this misunderstanding is probably due to the specimen's, pendent appearance which resulted from bending the scape during collecting or pressing. Aside from this factor, Mez's description of *V. ororiensis* falls well within the range of variation I have observed in populations of the montane, day flowering taxon which I treat as *V. ororiensis*. The type material also agrees well with collections from Volcán Irazu. I doubt that Oersted's collection was made at Orosi as indicated on the label because the elevation at Orosi is approximately 1000 m. This elevation is at least 900 m lower than the lowest elevation at which *V. ororiensis* has ever been encountered. The Oersted specimen was most likely collected on the slopes of Volcán Irazu, which he is known to have ascended.

Mez described *Vriesea crassiflora* from a Werckle collection that was reportedly made in the vicinity of Cartago. However, examination of the type specimen of *V. crassiflora* revealed a handwritten notation by Werckle on a field tag indicating that the collection was made in the vicinity of Coliblanco on the slopes of Irazu. Moreover, Werckle included several sketches of the flowers of *Vriesea crassiflora* at anthesis. These sketches, in conjunction with the character Mez (1934-1935) and Smith & Downs (1977) used to separate *Vriesea crassiflora* from *V. ororiensis*, penduncle length (which is variable in *V. ororiensis*), leave little doubt that this taxon is conspecific with *V. ororiensis*.

Based on his misinterpretation of scape orientation in *V. ororiensis* Mez described *V. irazuensis,* a species with erect inflorescences. Smith and Downs (1977) also distinguished *V. irazuensis,* from *V. ororiensis* on the basis of scape orientation. Other than this alleged difference in scape orientation, *V. irazuensis,* agrees in all critical characters with *V. ororiensis. Vriesea irazuensis* sensu L. B. Smith and Downs (1977), not Mez & Werckle (1903), is conspecific with *V. nephrolepis,* a night flowering taxon with an erect inflorescence.

Vriesea standleyi is well within the range of variability observed in *V. ororiensis* and consequently its maintenance as a distinct species is unsupportable. When Smith described *V. standleyi,* he misinterpreted its affinities by considering its closest relationship to be with *V. stenophylla,* a distinctly different taxon. In 1977, Smith and Downs also separated *V. standleyi* from *V. ororiensis* on the basis of a primary bract character. They considered the primary bracts of *V. standleyi,* to be densely pale lepidote, whereas they found those of *V. ororiensis* to be glabrous and even or verrucose. This type of difference is more a reflection of populational variation than it is of species differences.

In 1942 Suessenguth and Goeppinger (in Suessenguth, 1942) described two additional taxa from the Costa Rican collections of Kupper which are also synonyms of *V. ororiensis*. The first of these, *V. cylindracea,* was collected by Kupper near Canaan, apparently during his ascent of Cerro Chirripo. The type specimen has 2-flowered lateral branches, subcoriaceous floral bracts and stout pedicels. These characters, in conjunction with the marginal pubescence of the primary bracts (a character that I never observed in species of the pedicellate line), indicate that *V. cylindracea* is closest to *V. ororiensis* and *V. nephrolepis*, rather than *V. leptopoda (Thecophyllum rubrum)* and *V. latissima* to which it was compared by Suessenguth. Although Smith and Downs (1977) maintained this taxon on the basis of its primary bract development, it is best treated as a synonym of *V. ororiensis*, rather than *V. nephrolepis*, because of its relatively short petals and its primary bracts which are not rugose.

The second species described by Suessenguth and Goeppinger, *V. kupperi,* was based

on a specimen consisting of the upper part of a scape and an inflorescence. Because of the good color preservation, there is no doubt that the scape and primary bracts were originally a shade of red or pink. When this factor is considered with the size of the sepals and petal size and color, there is no doubt that *V. kupperi* is conspecific with *V. ororiensis*. This species was first placed in synonymy under *V. ororiensis* by Smith (1966).

In summary, *V. ororiensis* may be characterized by its erect inflorescence, red, crimson, or rarely pink primary bracts and its green-yellow, tubular, diurnal flowers. *V. ororiensis* is extremely difficult to distinguish from *V. nephrolepis* in fruiting or vegetative condition. This problem is discussed under the latter species.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: Volcán Poas, 1961, *Hobbs s.n.* (US); 2-4 km south of Volcán Poas on Hwy. 120, 11 March 1975, *Utley & Utley 1930* (CAS), *1931* (M), *1932* (DUKE), *1933* (CR), *1934* (F), *1935* (US), *1936* (MO), *1937* (NOLS), *1938* (MICH), *1939* (MEX), *1940 A* (GOET), *1941* (DUKE), *1942* (B), *1943* (WIS), *1944* (K), *1945* (L), *1946* (DUKE) & *1947* (C). CARTAGO PROVINCE: Volcán Irazu, 24 February 1957, *Carlson 3554* (US); 11 March 1894, *Donnell Smith 4963* (US); beyond Cartago, 15 December 1948, *Foster 2677* (US); 19 miles south of Cartago on Interamerican Highway, Talamanca Mountains, 10 July 1962, *Haines & Haines 697* (US); 22 miles south of Cartago on Interamerican Highway, north slopes of Talamanca mountains, north slopes of Talamanca mountains, 17 July 1962; *Haines & Haines 724* (US); 21 miles south of Cartago on Interamerican Highway, 19 July 1962, *Haines & Haines 731* (US); 29 miles south of Cartago on Interamerican Highway, 19 July 1962, *Haines & Haines 733* (US); 45 miles south of Cartago on Interamerican Highway, 23 July 1962, *Haines & Haines 740* (US); 48 miles south of Cartago on Interamerican Highway, 23 July 1962, *Haines & Haines 741* (US); 48 miles south of Cartago on Interamerican Highway, 28 July 1962, *Haines & Haines 745* (US); 50 miles south of Cartago on Interamerican Highway, 30 July 1962, *Haines & Haines 755* (US); 41 miles south of Cartago on Interamerican Highway, 30 July 1962, *Haines & Haines 757* (US); 34 miles south of Cartago on Interamerican Highway, 11 August 1962, *Haines & Haines 770* (US); 33 miles south of Cartago on Interamerican Highway, 11 August 1962, *Haines & Haines 772* (US); south slope of Volcan Irazu, on highway about 5 km northeast of Finca Robert, 26 June 1949, *Holm & Iltis 437* (US); upper slopes of Volcán Irazu on road from Cartago to summit, 7 April 1953, *Moore 6658* (US); southern slope of Volcán Irazu, from native collector, March 1924, *Standley 36631* (US); southern and eastern slopes of Volcán Irazu along Hwy. 8, 23 February 1974, *Utley & Utley 647* (DUKE, US, CR); 12 March 1975, *Utley & Utley 1953* (CR), *1954* (DUKE), *1955* (F), *1956* (CR); on old road off of the Interamerican Highway north of El Empalme, 16 April 1975, *Utley & Utley 2174* (DUKE), *2176* (CR); the southern slopes of Volcán Irazu on farm road leading from Hwy. 8 to Finca Coliblanco, 25 January 1976, *Utley & Utley 3815 A&B* (DUKE, CR), *3816 A&B* (US, DUKE), *2817 A&B* (F, MO), *3818* (GH), *3819* (NOLS), *3820* (MICH), *3821 A, B & C* (DUKE, US, B), *3824* (K), *3825* (DUKE), *3826* (WIS), *3827* (CAS), *3828* (NY), *3829* (DUKE), *3830 B* (NOLS, CR, MEX), *3831* (US) & *3832* (F); southern slope of Volcan Turrialba, 15 March 1976, *Utley & Utley 4309* (US), *4310* (DUKE), *4311* (CR), *4312* (DUKE), *4313* (NOLS), *4314* (US), *4315*(F), *4316* (MO), *4317* (MICH), *4318* (GH), *4319* (DUKE), *4322* (USF), *4323* (NO), *4324*(F), *4325* (DUKE), *4326* (B), *4327* (NY), *4328* (MO), *4329* (NOLS), *4330* (DUKE), *4331* (CAS), *4332* (BR) & *4333* (DUKE); cloud forest area between the paramillo of Cerro de la Muerte and Villa Mills, Cordillera de

Talamanca, 26 February 1965, *Williams et al. 28337* (US). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: 2-3 km west of Villa Mills on the Interamerican Highway, 17 March 1975, *Utley & Utley 1975* (DUKE), *1976* (CR), *1977* (US), *1979*(NOLS), *1980* (BM), *1981* (F), *1983* (MO), *1984* (MICH), *1985* (GH), *1986* (CAS), *1988* (NY), *1989* (WIS), *1990* (PMA), *1991*(C), *1992* (L); 27 April 1975, *Utley & Utley 2266* (DUKE);2-3 km west of Villa Mills on the Interamerican Highway, 5 April 1976, *Utley & Utley 4483* (DUKE) & *4484* (CR); at Villa Mills on the Interamerican Highway, 5 April 1976, *Utley & Utley 4487* (US), *4488* (NOLS), *4489* (MICH), *4490*(DUKE), *4491* (MO) & *4492* (DUKE); between Salispuedes and Ojo de Agua on the Interamerican Highway south of Cartago, 5 April 1976, *Utley & Utley 4496* (CR) & *4497* (DUKE). HEREDIA PROVINCE: summit of Volcán Barba within 1 km of Laguna Barba, 16 March 1975, *Utley & Utley 1961* (NOLS), *1962* (DUKE), *1963* (US), *1965*(F), *1966* (DUKE), *1967* (NY), *1968*(MO), *1969* (CAS), *1970* (MICH), *1971* (DUKE), & *1972* (NOLS); 12 April 1975 *Utley & Utley 2013* (DUKE), *2014* (CR), *2015* (US) *2023* (F), *2024* (MEX), *2039* (MO) & *2042* (DUKE); 25 January 1976, *Utley & Utley 3706* (DUKE), *3730* (CR), *3731* (DUKE); 5 March 1976, *Utley & Utley 4210* (DUKE), *4211* (CR), *4213* (DUKE), *4214* (F), *4215* (MO), *4216* (NOLS), *4217* (MICH), *4218 A&B*(GH, CAS), *4219* (MEX), *4220* (NY), *4221* (WIS), *4222* (DUKE), *4223* (C), *4224* (M), *4225* (MICH), *4226* (PMA), *4227* (DUKE), *4228* (F), *4229* (DUKE), *4230* (DUKE), *4232* (CAS), *4233* (NY), *4234* (CAS), *4235* (HEID), *4236* (DUKE), *4237* (MICH), *4238* (F), *4239* (US), *4240*(DUKE), *4255* (CR), *4256* (F), *4257* (DUKE); 9 April 1976, *Utley & Utley 4578* (NOLS), *4580* (DUKE) & *4581* (CR). SAN JOSÉ PROVINCE: on tree trunk north of San José , 5 March 1966, *Smith & Berry 15316* (US); on tree cloud forest, Aserrí, 19 April 1966, *Smith, L.B. 15327* (US); Cedral (Cerros de Escazú), approach to and upper slopes of Cerro Daser 3-5 km southwest of Aserrí, 30 April 1975, *Utley & Utley 2301* (DUKE), *2302* (DUKE), *2303* (CR), *2304* (DUKE) & *2305* (DUKE); 13 March 1976, *Utley & Utley 4261* (DUKE), *4262* (CR), *4267 A & B* (US, DUKE) *4268* (F), *4269* (MO), *4270* (MICH), *4272* (US),*4273* (NOLS), *4274* (DUKE), *4275* (CR), *4276* (NY), *4277* (CAS), *4278* (GH), *4279* (MO). PANAMÁ:- CHIRIQUÍ PROVINCE: Las Nubes, 7 August, *Croat 26471* (MO).

11. *Vriesea balanophora* (Mez) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

> *Guzmania balanophora* Mez in DC. Mon. Phan. 9: 918. 1896.
> TYPE: COSTA RICA. *Oersted Brom. n. 22.* (HOLOTYPE: C!, photograph US!).
>
> *Thecophyllum balanophorum* (Mez) Mez, Bull. Herb. Boiss. ser. II. 3: 131. 1903.
>
> *Thecophyllum lineatum* Mez & Werckle, Bull. Herb. Boiss. ser. II. 4: 875. 1904.
> TYPE: COSTA RICA: *Werckle "Bromel. Costaric." 114 and 16,260.* (LECTOTYPE: *Werckle 114*, B!, photograph US!; SYNTYPE: *Werckle Inst. Phys. -Geogr. Costar. 16260,* B!, photograph US!).
>
> *Thecophyllum balanophorum* var. *subpictum* Suesseng. Bot. Jahrb. 72: 291. 1942.
> TYPE: COSTA RICA. *Kupper 257.* (HOLOTYPE: M!, photograph US!).
>
> *Vriesea lineata* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

Epiphytic or rarely terrestrial, acaulescent to 20.0 cm caulescent. LEAVES in a sub-

speading to subascending rosette, (19.0) 22.0-31.2 cm long; *blades* 12.0-23.0 cm long and 1.8-2.9 cm wide, green with maroon wavy cross bands and occasionally with maroon longitudinal lines proximally, subligulate to broadly triangular, apex acute to acuminate or attenuate; *sheaths* (6.8) 7.6-9.8 cm long and 3.2-5.0 cm wide, castaneous, usually darker abaxially, with a coating of cinereous trichomes and frequently longitudinal maroon lines distally, elliptic or rarely obovate. SCAPE erect or curved-erect (26.0) 33.0-40.0 (48.0) cm long and 0.2-0.3 cm in diameter; *bracts* 4.0-10.0 (17.7) cm long and 0.4-2.1 cm wide, green or green suffused with maroon, usually with maroon wavy transverse lines and a covering of cinereous trichomes, clasping-erect in sheath area becoming spreading in the area of blade, triangular to subligulate, apex acute and attenuate. INFLORESCENCE erect, 3.0-6.0 (9.0) cm long and 3.0-7.0 cm in diameter, cylindric, glabrous occasionally with brown-margined punctulae; *primary bracts* 3.0-6.2 cm long and 1.4-2.0 (2.8) cm wide, spreading to subascending, green with maroon wavy cross-bands, occasionally suffused with red or maroon, triangular, apex acute to acuminate or attenuate. LATERAL BRANCHES subspreading or spreading, collaterally 2-flowered, peduncles 0.2-0.5 cm long. FLOWERS sessile to less than 0.1 cm pedicellate; *floral bracts* 0.9-1.2 cm long and 1.0-1.5 cm wide, subcoriaceous green frequently suffused with maroon or completely maroon, drying to brown,surface finely nerved, minutely pitted or brown-margined punctulate, keeled, broadly elliptic to suborbicular, apex rounded to obtuse, frequently incised; *sepals* 1.0-1.3 cm long and 0.8-1.1 cm wide, green suffused with maroon, entirely maroon or castaneous, coriaceous, elliptic, apex rounded, frequently minutely incised; petals 1.9-2.0 cm long and 1.0-1.1 cm wide, white more or less obovate; *appendages* 0.3-0.4 cm long and 0.2 cm wide; *stamens* in hood configuration over the stigma, anthers not laterally connivent, filaments 1.2-1.4 cm long, anthers 0.4 cm long; *ovary* 0.3-0.4 cm long and 0.3-0.4 cm in diameter, style about 1.2 cm long; *capsule* 1.7-2.5 cm long and 0.7-1.0 cm in diameter, subfusiform to obovate, maroon becoming castaneous when mature.

PHENOLOGY: *V. balanophora* has been collected in flower during the months of August and December. That these two months represent a sample of a flowering season extending through the heavy rain months of September, October and November is difficult to believe. Rather, the species probably flowers sporadically throughout the "dry" season of January through April (May) and the early rainy season of JuneJuly.

DISTRIBUTION AND HABITAT: The species is endemic to Costa Rica where it is known from the volcanos of the Cordillera Central and the northern extension of the Cordillera de Talamanca. The species has been collected between 1500-1900 m in the lower montane and premontane rain forest life zones and possibly extends slightly into the lower montane wet forest life zone.

DISCUSSION: *V. balanophora* is easily distinguished from other vrieseas by its cinereously pubescent leaves with wavy maroon transverse lines and erect inflorescences bearing white, crepuscular flowers with campanulate corollas.

Although the type of *V. balanophora* is poorly preserved, there is no doubt that *V. lineata* is conspecific with it. Judging from the type, Mez's interpretation of the orientation of the scape apparently was in error. At first glance, the scape appears pendulous but this is a result of its having been broken and bent to facilitate mounting or pressing. In its natural state, it was obviously erect or curved-erect. Suessenguth and Goeppinger (1942) described *T. balanophorum* var. *subpictum* on the basis of its shorter leaves which were suffused with red and red

wavy crossbands. However, the type of *T. balanophorum* var. *subpictum* is well within the range of variation that I have observed in *V. balanophora* and is undeserving of recognition at the varietal level.

Vriesea balanophora is most similar vegetatively to *V. leucophylla*. Because of their overlapping distributions and almost identical leaf pubescence and markings, the taxa are frequently difficult or impossible to separate in the vegetative condition. In flower or fruit the species are easily separated by a number of characters, the most conspicuous of which is inflorescence orientation. Inflorescences of *V. balanophora* are erect, in contrast to the pendent inflorescences of *V. leucophylla*. The primary bracts of the former taxon are also shorter than those of the latter species. Moreover, the floral syndromes of these species are different. As I indicated prevously, *V. balanophora* has campanulate, crepuscular flowers; this differs markedly from the chartreuse, more or less tubular, diurnal flowers characteristic of *V. leucophylla*.

Vriesea balanophora may be most closely related to *V. luis-gomezii*, but their relationship cannot be fully interpreted until more material of this latter poorly known taxon is available. These two species share a number of characters including nocturnal or crepuscular white, campanulate flowers and leaves with cinereous pubescence and wavy transverse lines. The two taxa are currently separated on the basis of the longer floral bracts (1.5-1.7 cm) and sepals (1.5-1.6 cm) of *V. luis-gomezii* as opposed to the shorter floral bracts (0.9-1.2 cm) and sepals (1.0-1.3 cm) of *V. balanophora*.

SPECIMENS EXAMINED: COSTA RICA: PROVINCE OF ALAJUELA: about 3-4 km west of the junction of highways 9 and 120 on Highway 120; the saddle between Volcan Poas and Volcan Barba, 27 March 1976, *Utley & Utley 4338* (NOLS). BORDER OF ALAJUELA AND HEREDIA PROVINCES: on the finca of Mike Canon at Vara Blanca, near the junction of highways 9 and 120, 20 July 1975, *Utley & Utley 2661* (DUKE). CARTAGO PROVINCE:- Tapantí Hydroelectric Project, slopes overlooking the Río Grande de Orosí about 5 km beyond the entrance to the Project, 22 March 1976, *Utley & Utley 4354* (DUKE) & *4355* (NY). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: along the Interamerican Highway southeast of Casa Mata or 10-12 km south of San Isidro de Cartago, 17 March 1975, *Utley & Utley 2000* (US), *2001* (DUKE) & *2002* (CR); 3 August 1975, *Utley & Utley 2756* (CAS) & *2757* (DUKE); 5 September 1975, *Utley & Utley 3086* (DUKE). HEREDIA PROVINCE: Cerro de Las Lajas, north of San Isidro, 7 March 1926, *Standley & Valerio 51496* (US); Cerro de Las Caricias north of San Isidro, 11 March 1926, *Standley & Valerio 52325* (US); region north of Cerro Chompipe about 15 km northeast of Heredia and 3 km north of Cerro Redondo de La Cruz, 15 October 1974, *Utley & Utley 1312* (DUKE). SAN JOSÉ PROVINCE: region between Cascajal and about 8 km northeast on Highway 216, 23 August 1975, *Utley & Utley 2917* (DUKE), *2918* (CR) & *2945* (NOLS); 10 December 1975, *Utley & Utley 3601* (MO), *3619* (F) & *3620* (DUKE); Altos de Tablazo, about 5 km southeast of Higuito on Calle Tablazo, or about 12 km southeast of Desamparados, *Utley & Utley 3871* (DUKE) & *3872* (NOLS); 9 May 1976, *Utley & Utley 4736* (DUKE); 4 km north of Cascajal or 7 km north of Las Nubes on Hwy 216 near the road terminus, 3 July 1976, *Utley & Utley 5263* (US), *5269* (DUKE) & *5270* (CR, F).

12. *Vriesea luis-gomezii* Utley, sp. nov. Fig. 21.

A *V. balanophora* (Mez) L. B. Smith & Pitt. cui valde affinis, bracteis florigeris et sepalis longioribus differt.

Epiphytic acaulescent to short caulescent. LEAVES in a spreading to subascending rosette, 33.6-43.2 cm long; *blades* 17.3-27.3 cm long and 3.5-4.0 cm wide, red suffused with areas of green, and with reddish-purple or dark wavy transverse lines, occasionally with longitudinal reddish-purple lines proximally, ligulate, apex acute to acuminate or attentuate; *sheaths* 14.0-16.6 cm long and 6.6-7.1 cm wide, dark castaneous abaxially, brown adaxially, frequently suffused with purple-maroon wavy transverse lines distally, elliptic in outline. SCAPE erect, 48.5-62.0 cm long and 0.4-0.5 cm in diameter; *bracts* 5.9-9.1 cm long and 2.8-3.2 cm wide, sheath and blade not strongly differentiated, blades green or green deeply suffused with red and with red wavy transverse lines proximally, erect, divergent distally, triangular, apex acute to attenuate, sheaths green with red longitudinal lines proximally and occasionally with wavy transverse lines distally, sheathing erect, ovate to elliptic. INFLORESCENCE erect, 9.0-15.5 cm long and 4.5-7.0 cm in diameter, cylindric, rachis red; *primary bracts* 5.0-8.2 cm long, blade and sheath frequently weakly differentiated, blades about 2.7-3.9 cm long and 1.8 cm wide, green frequently with wavy red transverse lines proximally, spreading to recurved or occasionally spirally involute, triangular, apex acute to attenuate, sheaths about 2.3-3.2 cm long and 2.7-3.2 cm wide, green with red longitudinal lines proximally or red wavy transverse lines distally, ovate. LATERAL BRANCHES spreading, to 2.5 cm long, collaterally 2-flowered peduncle 0.2-0.4 cm long, rachis wanting to 0.2 cm long. FLOWERS sessile to 0.3 cm pedicellate; *floral bracts* 1.5-1.7 cm long and 1.7-1.9 cm wide, maroon or green suffused with maroon marginally, subcoriaceous, brown-centered lepidote adaxially, glabrous abaxially, even or keeled, ovate or oblong-ovate to suborbicular, apex obtuse to broadly rounded, occasionally incised or torn medially; *sepals* 1.5-1.6 cm long and 1.0-1.2 cm wide, maroon or green, coriaceous, brown-centered lepidote adaxially, glabrous abaxially, elliptic incised; *petals* about 2.9 cm long and 1.1-1.2 cm wide, white, obovate, appendages 0.4 cm long and 0.2 cm wide; *stamens* in hood configuration over the gynoecium, filaments about 2.1 cm long, anthers 0.6 cm long; *ovary* 0.5 cm long, style 2.7 cm long.

TYPE: COSTA RICA: CARTAGO: on foot or beast path off the old Pan American Highway about 1-2 km north of El Empalme in the Cordillera de Talamanca, elev. 2000-2100 m, 10 May 1975, *Utley & Utley 2460* (HOLOTYPE: DUKE!, ISOTYPES: CR!, F!, DUKE!, US!).

PHENOLOGY: Flowering specimens collected in May.

DISTRIBUTION AND HABITAT: Known only from the type location in Costa Rica at 2000-2100 m in the lower montane rain forest life zone.

DISCUSSION: *Vriesea luis-gomezii* is a poorly known but distinct species, easily recognized on the basis of its green leaves with longitudinal and transverse red-purple to dark red lines and spreading to subspreading rosette. The floral bracts which are about equal in length to the maroon sepals, are maroon or green suffused with maroon. Flowers of this taxon are white, campanulate and nocturnal or crepuscular.

Since this taxon is only known from a few collections, any definitive analysis of its affinities must await additional field work. However, *V. luis-gomezii* appears to be most closely allied to *V. balanophora*. This is presented in greater detail under the discussion of *V. balanophora*.

ETYMOLOGY: This species is named in honor of Luis Diego Gomez P., pteridologist and former Director of the Museo Nacional de Costa Rica.

SPECIMENS EXAMINED: COSTA RICA: CARTAGO PROVINCE: on horse trail northeast of the old Pan

American Highway 1-2 km north of El Empalme, 16 April 1975, *Utley & Utley 2184* (NOLS).

13. *Vriesea viridis* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953.

Thecophyllum viride Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 872. 1904.

TYPE: COSTA RICA: near Desengano, *Werckle s.n.* (HOLOTYPE: B!, photograph US!).

Epiphytic or terrestrial, acaulescent or caulescent to 20.0 cm. LEAVES in a subspeading to subascending rosette, (28.0) 31.0-46.0 (63.0) cm long; *blades* 16.8-33.0 (46.5) cm long and (3.1) 4.0-5.7 cm wide, green occasionally suffused with maroon or red-maroon at the apices and margins, with fine

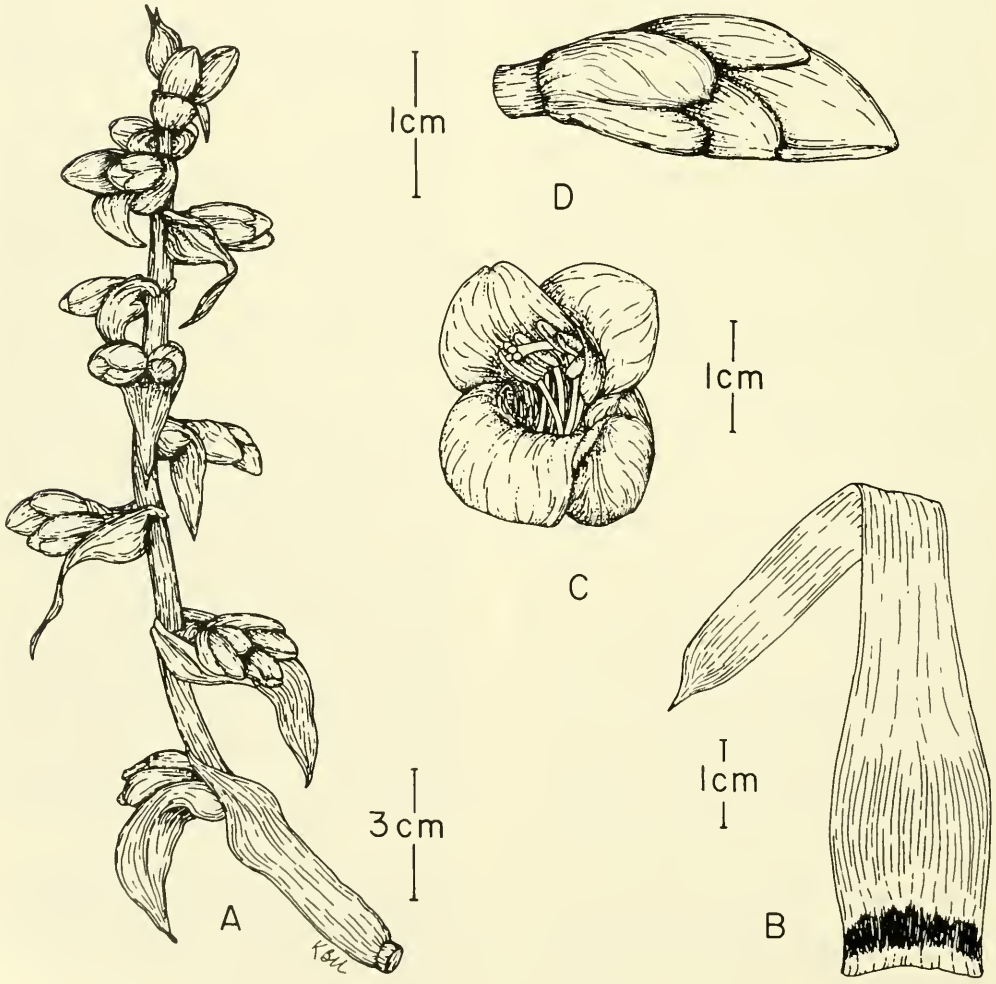


Fig. 21. *Vriesea luis-gomezii*. A. Inflorescence; B. Leaf; C. Flower D. Nearly mature fruit with sepals and floral bract. From *(Utley & Utley 2467)*.

wavy, dark green cross bands, these occasionally suffused with red-maroon or entirely red-maroon, ligulate to subligulate or broadly triangular, apex acute to acuminate or attenuate; *sheaths* (9.6) 12.4-18.0 (20.0) cm long and (4.4) 6.0-8.4 cm wide, pale white with a layer of cinereous trichomes on the upper and lower surfaces, frequently with an abaxial castaneous area or rarely both surfaces castaneous, elliptic to obovate. SCAPE erect to curved-erect (27.0) 36.0-60.0 cm long and 0.3-0.6 cm in diameter; *bracts* erect to spreading or the uppermost recurved, 5.5-15.0 (19.0) cm long, blades 3.0-10.4 (15.2) cm long and (0.9) 1.2-2.5 (3.0) cm wide, lowermost colored like leaves, middle and upper with red-maroon transverse lines and frequently suffused with red-maroon, triangular to broadly triangular or ligulate, apex acute to acuminate or attenuate, sheaths 2.1-4.0 (4.8) cm long and 2.0-4.2 cm wide, red-maroon becoming yellow near junction with blade but occasionally ochre or entirely red-maroon, ovate or elliptic to obovate or suborbicular. INFLORESCENCE erect, 11.0-31.0 cm long and 4.5-7.5 cm in diameter, cylindric, rachis glabrous occasionally with dark castaneous punctulae; *primary bracts* 5.0-10.0 (13.0) cm long, spreading or reflexed at the blade-sheath junction, blades (2.4) 3.0-7.0 (9.7) cm long and 0.8-2.2 (2.8) cm wide, green to pink, red or maroon, with wavy cross bands, these usually suffused with red or maroon, triangular to broadly triangular, apex acute to attenuate, sheaths (2.2) 2.8-3.6 cm long and (2.2) 2.6-3.6 cm wide, red or red-maroon frequently becoming yellowish near the junction with blade, drying to ochre or brown, elliptic to broadly elliptic or ovate. LATERAL BRANCHES spreading, collaterally 2-flowered, peduncles 0.0-0.4 (0.9) cm long, rachis wanting. FLOWERS 0.3-1.3 cm pedicellate; *floral bracts* 0.5-1.1 cm long and 0.6-1.3 cm wide, green usually suffused with maroon, subcoriaceous, keel frequently inflated or creased, surface even to obscurely nerved or pitted, with castaneous to light brown punctulae especially basally and on the keel, ovate to elliptic, apex acute or acuminate to obtuse or broadly rounded, frequently torn or appearing incised; *sepals* 1.1-1.6 cm long and 0.8-1.3 cm wide, green suffused with maroon, or completely maroon, coriaceous, elliptic to obovate, apex rounded to obtuse, frequently emarginate or torn-incised; *petals* 1.9-2.5 cm long and 1.1-1.4 cm wide, white to greenish-white, obovate to elliptic; *appendages* 0.4-0.5 cm long and 0.2 cm wide; *stamens* arranged in a hood over the gynoecium, anthers laterally connivent, filaments 1.9-2.1 cm long, anthers 0.4-0.5 cm long; *ovary* 0.4-0.5 cm long and 0.3-0.5 cm in diameter, style 1.5-1.8 cm long; *capsule* 3.0 cm long and 0.8 cm in diameter, castaneous subfusiform to obovate.

PHENOLOGY: Flowering specimens have been collected during March and April.

DISTRIBUTION AND HABITAT: Endemic to the vicinity of Volcán Barba in the Cordillera Central de Costa Rica between 1800-2100 m in the lower montane rain forest life zone.

DISCUSSION: *V. viridis* is a narrow endemic which can be locally abundant and even weedy in some areas. It is distinguished by an erect inflorescence, maroon sepals and white, crepuscular flowers in which the corollas are geniculate-tubular.

This taxon is most similar to *V. balanophora* and *V. luis-gomezii* from which it is distinguished by floral bract and inflorescence length as well as its geniculate-tubular corolla. In sterile or fruiting condition, this species can be confused with both *V. ororiensis* and *V. nephrolepis* from which it can generally be distinguished by the cinereous pubescence of the abaxial leaf surface as well as the tendency for the leaves to be broad triangular in outline, in contrast to the ligulate or subligulate leaf blades of the other two taxa.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: between

the junction of highways 9 and 120 and the summit of Volcán Poas, 11 March 1975, *Utley & Utley 1915* (CR), *1916* (GH), *1917* (DUKE), *1919* (NOLS), *1920* (K), *1923* (CR), *1925* (F) & *1926* (DUKE). HEREDIA PROVINCE: region north of Cerro Chompipe, about 15 km northwest of Heredia and 3-5 km north of Cerro Redondo de La Cruz, 15 October 1974, *Utley & Utley 1292* (NOLS); 13 April 1975, *Utley & Utley 2086* (CR), *2089* (DUKE), *2090* (NOLS), *2091* (US), *2092* (F), *2093* (DUKE) & *2094* (MO); about 1-3 km south of the junction of highways 9 and 120, on slopes above the Río Desengano, 11 May 1975, *Utley & Utley 2481* (DUKE) & *2483* (US); road north of Hwy. 113 connecting with Calle Gallito, saddle area between Cerro Chompipe and the southeast flank of Volcán Barba, 25 October 1975, *Utley & Utley 3201* (DUKE); 8 December 1975, *Utley & Utley 3580* (DUKE); 2-3 km south of the junction of highways 9 and 120 on Hwy. 9, slopes above the Río Desengano, 27 March 1976, *Utley & Utley 4377* (CR), *4380* (NOLS), *4381* (US), *4388* (F), *4389* (MO), *4390* (NY), *4397* (CAS), *4398* (DUKE) *4399* (B), *4400* (CR), *4401* (MICH), *4402* (MO), *4403* (DUKE), *4404* (DUKE) *4405* (US), & *4408* (MEXU); approach to the southeastern flank of Volcán Barba on the southwest side of Cerro Chompipe, 1 April 1976, *Utley & Utley 4421* (CR), *4422* (DUKE), *4423* (DUKE), *4425* (NY), *4426* (CAS), *4427* (US), *4428* (BM), *4429* (MO), *4430* (DUKE), *4431* (NOLS), *4437* (DUKE), *4438* (DUKE), *4440* (F), *4441* (US), *4442* (GH), *4443* (DUKE), *4444* (CR), *4445* (CAS), *4446* (B), *4447* (DUKE). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: about 5 km northeast of San Isidro de Heredia along the banks of the Río Para Blanco and on the lower slopes of Cerro Zurquí, 30 March 1974, *Utley & Utley 736* (DUKE), *737* (US), & *750A* (CR); 21 October 1975, *Utley & Utley 3177* (DUKE); about 5 km northeast of San Isidro de Heredia on Calle Yerbabuena, 3 April 1976, *Utley & Utley 4476* (DUKE).

14. *Vriesea hainesiorum* L. B. Smith, Phytologia 8: 498. 1963

TYPE: COSTA RICA: CARTAGO PROVINCE: Interamerican Highway, 6 miles south of Cartago, Talamanca Mountains, elev. 1650 m, *Haines & Haines 682* (HOLOTYPE: US!).

Epiphytic acaulescent. LEAVES in an ascending rosette, 14.0-21.0 (27.0) cm long; *blades* 9.0-13.0 (19.0) cm long and 0.8-1.4 cm wide, green, narrowly triangular, apex attenuate; *sheaths* (3.5) 4.5-6.5 (8.0) cm long and 2.2-3.4 cm wide, green densely cinereously pubescent, margins purple, dark maroon or castaneous, elliptic. SCAPE decurved, usually crimson, (16.0) 20.0-25.0 cm long and about 0.1-0.2 cm in diameter; *bracts* divergent to spreading (3.5) 4.2-8.4 (10.1) cm long, blades 1.5-8.0 cm long and 0.2-0.6 cm wide, green or green suffused with red, occasionally crimson, narrowly triangular to setiform, apex attenuate to long acuminate, sheaths 1.8-3.0 cm long and 0.9-1.4 cm wide, green suffused with red to crimson, clasping erect, elliptic to ovate. INFLORESCENCE pendent, 3.0-6.0 cm long and 3.0-7.0 cm in diameter, more or less cylindric, rachis geniculate, crimson, *primary bracts* spreading 3.4-5.3 (6.5) cm long, blades 1.4-3.2 cm long and 0.2-0.7 cm wide, green suffused with red to crimson, drying to brown, narrowly triangular to setiform, apex attenuate. LATERAL BRANCHES divergent to spreading, 0.5-0.7 cm long, collaterally 2-flowered, peduncles 0.2-0.3 cm long, rachis 0.2-0.3 cm long. FLOWERS sessile to 0.2 cm pedicellate; *floral bracts* (1.3) 1.5-1.8 cm long and 1.4-1.9 cm wide, pale green drying to brown, subcoriaceous to coriaceous, finely nerved with scattered punctulae, keel prominently folded or inflated, elliptic to ovate or suborbicular, apex obtuse to rounded, frequently torn-incised;

sepals 1.9-2.1 cm long and 1.1-1.4 cm wide, pale green, drying to brown, coriaceous, elliptic to obovate, apex obtuse to rounded, frequently torn-incised; *petals* 2.7-2.8 cm long and 0.9-1.0 cm wide, greenish-yellow, obovate; *appendages* 0.4 cm long and 0.15-0.2 cm wide; *stamens* in a hood configuration over gynoecium, filaments about 2.0 cm long, anthers 0.3-0.35 cm long; *ovary* 0.4 cm long and 0.3 cm in diameter, style about 1.9 cm in diameter, green becoming castaneous.

PHENOLOGY: Flowering specimens have been collected during the month of May.

DISTRIBUTION AND HABITAT: Endemic to the northern extension of the Cordillera de Talamanca in Costa Rica. Collected between 1700-1900 m in the lower montane wet and lower montane moist forest life zone.

DISCUSSION: *Vriesea hainesiorum* is a distinctive taxon which is characterized by narrowly triangular leaves with attenuate apices borne in an ascending rosette. Inflorescences are decurved to pendent and highly colored. Both the scape and primary bracts are deep red to crimson, and the flowers are diurnal, greenish yellow and tubular. *V. hainesiorum* is most closely related to *V. leucophylla*, from which it is easily distinguished by its ascending rosette, unmarked, short, narrowly triangular leaves and few-flowered inflorescence (ten or fewer flowers). The relationship of *V. hainesiorum* to *V. leucophylla* is discussed in greater detail under *V. leucophylla*.

SPECIMENS EXAMINED: COSTA RICA: CARTAGO: 5-6 km south of San Isidro de Cartago on the Pan American Highway, 1700-1800 m, 28 February 1975, *Utley & Utley 1908* (DUKE). SAN JOSÉ: on road to Tablazo ca. 1-2 km from crest of Altos de Tablazo or 5-6 km SE of Higuito or 12-14 km SE of Desamparados, 1700-1800 m, 5 September 1975, *Utley & Utley 3062* (CR), *3063* (US), *3064* (DUKE) & *3065* (NOLS); 30 January 1976, *Utley & Utley 3864* (DUKE), 3865 (MO), *3866* (NY) & *3867* (F); 9 May 1976, *Utley & Utley 4738A* (NOLS), *4741* (CR), *4742* (CAS), *4780* (GH), *4781* (F) & *4785* (DUKE): 2 July 1976, *Utley & Utley 5205* (DUKE).

15. *Vriesea leucophylla* L. B. Smith, Phytologia 8: 498. 1963

TYPE: COSTA RICA: CARTAGO PROVINCE: rock outcrop 11 miles south of Cartago, on Interamerican Highway, Talamanca Mountains, elev. 1860 m, *Haines & Haines 693* (HOLOTYPE: US!).

Vriesea leucophylla var. *subtessellata* Utley, Journ. Bromeliad Society 24: 16-18. 1974.
TYPE: COSTA RICA: SAN JOSÉ PROVINCE: southern slopes of Cerro Zurquí, 4.0-4.5 km north of San Isidro de Heredia, alt. 1800 m.
John & Kathy Utley 401 (HOLOTYPE: DUKE!, photographs CR!, US!).

Epiphytic or rarely terrestrial, acaulescent. LEAVES in a spreading to subascending rosette, 21.0-41.0 cm long; *blades* 13.0-29.0 cm long and 2.1-2.8 cm wide, green with dark green or maroon wavy transverse lines, ligulate to long triangular, apex attenuate to acute; *sheaths* 7.5-15.0 cm long and (3.9) 4.6-5.7 cm wide, pale brown to brown with a mosiac-like cover of brown to castaneous centered trichomes, usually suffused with purple or maroon wavy transverse lines in the distal portion, elliptic to ovate or subovate. SCAPE strongly decurved, 23.0-44.0 cm long and 0.3-0.5 cm in diameter; *bracts* erect, divergent distally, 6.0-18.0 cm long, blades 3.5-14.5 cm long and 0.8-2.1 cm wide, lowermost green and foliaceous, middle and upper suffused deep red-pink to crimson, usually with dark red or crimson wavy trans-

verse bands, subligulate to long triangular, apex acute to attenuate, sheaths clasping-erect, 2.2-4.2 cm long and 1.5-3.0 (3.3) cm wide, deeply suffused red-pink to crimson, ovate to elliptic in outline. INFLORESCENCE pendent (12.0) 20.0-34.0 cm long and 5.0-14.0 (19.0) cm in diameter, cylindric, to more or less conical, rachis red or crimson; *primary bracts* strongly spreading, geniculately reflexed at the blade-sheath junction, 6.0-13.5 cm long, occasionally with wavy transverse bands, subligulate to long triangular, apex acute to attenuate, sheaths 2.4-3.4 cm long and (1.9) 2.6-3.8 cm wide, deep red to crimson, ovate in outline. LATERAL BRANCHES spreading, 1.02.2 cm long, 2-flowered, or rarely 3-flowered, penduncles 0.7-1.5 cm long, rachis 0.2-0.5 cm long, flowers borne subcollaterally or if spikes 3-flowered then apparently pinnate. FLOWERS sessile to 0.3 cm pedicellate; *floral bracts* 1.4-2.0 cm long and 1.8-2.6 cm wide, subcoriaceous, green or rarely suffused with light pink, brown punctate or immersed lepidote abaxially, lepidote abaxially, oblong to elliptic or ovate, apex obtuse to broadly rounded and minutely apiculate, entire to deeply torn-incised along the conspicuous, frequently inflated keel; *sepals* 1.5-1.9 cm long and 0.9-1.5 cm wide, coriaceous, usually keeled, glabrous abaxially, lepidote adaxially, green to yellowgreen or strongly suffused with red at anthesis, elliptic to obovate, apex obtuse to rounded, occasionally torn incised; *petals* 2.4-2.9 cm long and 0.8-0.9 cm wide, greenish, elliptic to obovate, frequently subpandurate; *appendages* (0.2) 0.5-0.6 cm long and 0.1-0.2 cm wide; *stamens* in a hood configuration over gynoecium, filaments 1.8-2.1 cm long, anthers 0.4-0.6 cm long; *ovary* 0.4-0.5 cm long and 0.3-0.4 cm in diameter, style 1.6-1.8 cm long; *capsules* 3.7-4.0 cm long and about 0.9 cm in diameter, olive-brown, fusiform.

DISCUSSION: The features that characterize *Vriesea leucophylla* are its pendent, multiflowered inflorescence (more than 14 flowers) with red to crimson scape and primary bracts and floral bracts which are about as long as, or only slightly shorter than the sepals. The flowers of this taxon are diurnal, green-yellow and tubular.

Vriesea leucophylla is most closely related to *V. hainesiorum* and *V. vietoris*. It differs from the former species in leaf size and shape. The relationship of *V. leucophylla* to *V. vietoris* is discussed under the latter taxon.

DISTRIBUTION: The Cordillera Central of Costa Rica and the Cordillera de Talamanca in Costa Rica and northwest Panamá in the lower montane rain forest.

PHENOLOGY: Flowering June-August.

SPECIMENS EXAMINED: COSTA RICA: BORDER OF ALAJUELA AND-HEREDIA PROVINCES: Vara Blanca, the finca of Mike Canon, near the junction of highways 9 and 120, 1900 m, 20 July 1975, *Utley & Utley 2658* (F) & *2660* (DUKE). CARTAGO PROVINCE: 6 miles south of Cartago on the Interamerican Highway, Talamanca Mountains, 5500 feet, 10 July 1962, *A. Lee & Bruce L. Haines 679* (CR, US); region north of Muneco or about 5.5 km west of Orosí, 1600m, 18 October 1974, *Utley & Utley 1440* (DUKE). BORDER-OF CARTAGO AND SAN JOSÉ PROVINCES: about 20 km south of Cartago on the Interamerican Highway in the vicinity of Casa Mata, 1900 m, 17 March 1975, *Utley & Utley 1999* (DUKE), 3 August 1975, *Utley & Utley 2758* (US), *2759* (DUKE) & *2761* (NOLS), 24 August 1975, *Utley & Utley 2951* (DUKE). HEREDIA PROVINCE: vicinity of Vara Blanca in pastures along C.R. highways 9 and 120, 1900 m, 21 June 1976, *Utley & Utley 5146* (US), *5147* (CR), *5148* (NOLS), *5149* (F), *5150* (DUKE), *5151* (MO) & *5152* (DUKE). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: about 5 km northeast of San Isidro de Heredia along the banks of the Río Para Blanco

and on the lower slopes of Cerro Zurquí, 1500-1700 m, 10 June 1974, *Utley & Utley 933* (CR) & *955* (DUKE); 18 June 1974, *Utley & Utley 961* (DUKE), *962* (US) & *965* (DUKE); 22 December 1974, *Utley & Utley 1749* (F), *1750* (DUKE), *1751* (US) & *1752* (CR); 12 July 1975, *Utley & Utley 2613* (US) & *2614* (DUKE); 21 October 1975, *Utley & Utley 3176* (DUKE); 27 December 1975, *Utley & Utley 3665* (DUKE). SAN JOSÉ PROVINCE: Alto de la Palma, on Finca Porvenir, 18 August 1975, *Utley & Utley 2912* (DUKE); between 2 and 5 km southeast of Higuito on Calle Tablazo or between 8 and 12 km southeast of Desamparados, 1800-1900 m, 5 September 1975, *Utley & Utley 3066 A&B* (NOLS, DUKE). PANAMÁ: CHIRIQUI PROVINCE: Bajo Chorro, 13 February 1938, *Davidson 281* (F).

16. *Vriesea vietoris* Utley, Brittonia, 33: 584-586. 1981. Fig. 22

TYPE: COSTA RICA: BORDER OF CARTAGO AND SAN JOSE PROVINCES: pasture along the Interamerican Highway, 200 yards SE of Casa Mata in the Cordillera de Talamanca S of Cartago, 1800-1900 m *Utley & Utley 4747* (HOLOTYPE: DUKE!)

Plants acaulescent, epiphytic. LEAVES in a spreading to subascending rosette, 29-40 cm long; *blades* 19-29 cm long and 1.4-2.6 cm wide, green, occasionally suffused with maroon at margins and tips, densely pubescent on abaxial surface, subligulate to long-triangular apex attenuate or acuminate; *sheaths* 10-12.2 cm long, 3.4-5.2 cm wide, brown with a dense mosaic-like coating of castaneous-centered trichomes usually suffused with purple in the distal half, especially near the margins, elliptic to ovate in outline. SCAPE strongly decurved, 25-44 cm long, 0.3-0.5 cm diameter; *bracts* erect, divergent distally, 11-18 cm long, blades 7.4-14.4 cm long and 0.8-1.7 cm wide, lowermost green, middle and upper suffused deep red-pink to crimson, subligulate to long-triangular, apex attenuate to acute sheaths clasping erect, 2.2-4.2 cm long and 1.5-2.4 (3.3) cm wide, suffused red-pink to crimson, ovate. INFLORESCENCE pendent, 20-34 cm long and 10-14 (19) cm in diameter, subcylindrical to subconical, rachis deep reddish-pink to crimson; *primary bracts* scalariform-spreading, 8.5-13.5 cm long and 2.0-2.4 cm wide, deep red or crimson, ovate in outline. LATERAL BRANCHES spreading, 1-1.8 cm long, subcollaterally 2-flowered, peduncles 0.7-1.5 cm long, rachis 0.2-0.4 cm long. FLOWERS sessile or pedicels to 0.3 cm long; *floral bracts* 1.6-2 cm long and 1.5-2 cm wide, subcoriaceous, deep pink to crimson, minutely pitted, or brown-punctate abaxially, lepidote adaxially, oblong to elliptic or ovate-truncate, apex obtuse to broadly rounded and minutely apiculate, entire or torn-incised up to one-half the length at anthesis, keel inflated; *sepals* 1.6-1.9 cm long and 1.2-1.5 cm wide, coriaceous, keeled, glabrous abaxially, lepidote to rounded; *petals* 2.8-3 cm long and 0.8-1 cm wide, pale greenish-white, obovate to subpandurate; *appendages* 0.5-0.6 cm long and 0.2 cm wide; *stamens* forming a hood over the style, filaments 2.0-2.1 cm long, anthers 0.4 cm long; *ovary* 0.3-0.4 cm long and 0.4 cm in diameter, style 1.5-1.7 cm long.

PHENOLOGY: Flowering April and May.

DISTRIBUTION: Known only from the northern part of the Cordillera de Talamanca in Costa Rica in the lower montane wet forest at 1800-2100 m elevation.

DISCUSSION: The features which characterize *V. vietoris* are its unbanded leaves, pendent, many-flowered inflorescence (14 or more flowers) subscalariform primary bracts and floral bracts which are equal or subequal to the brightly colored sepals. The flowers

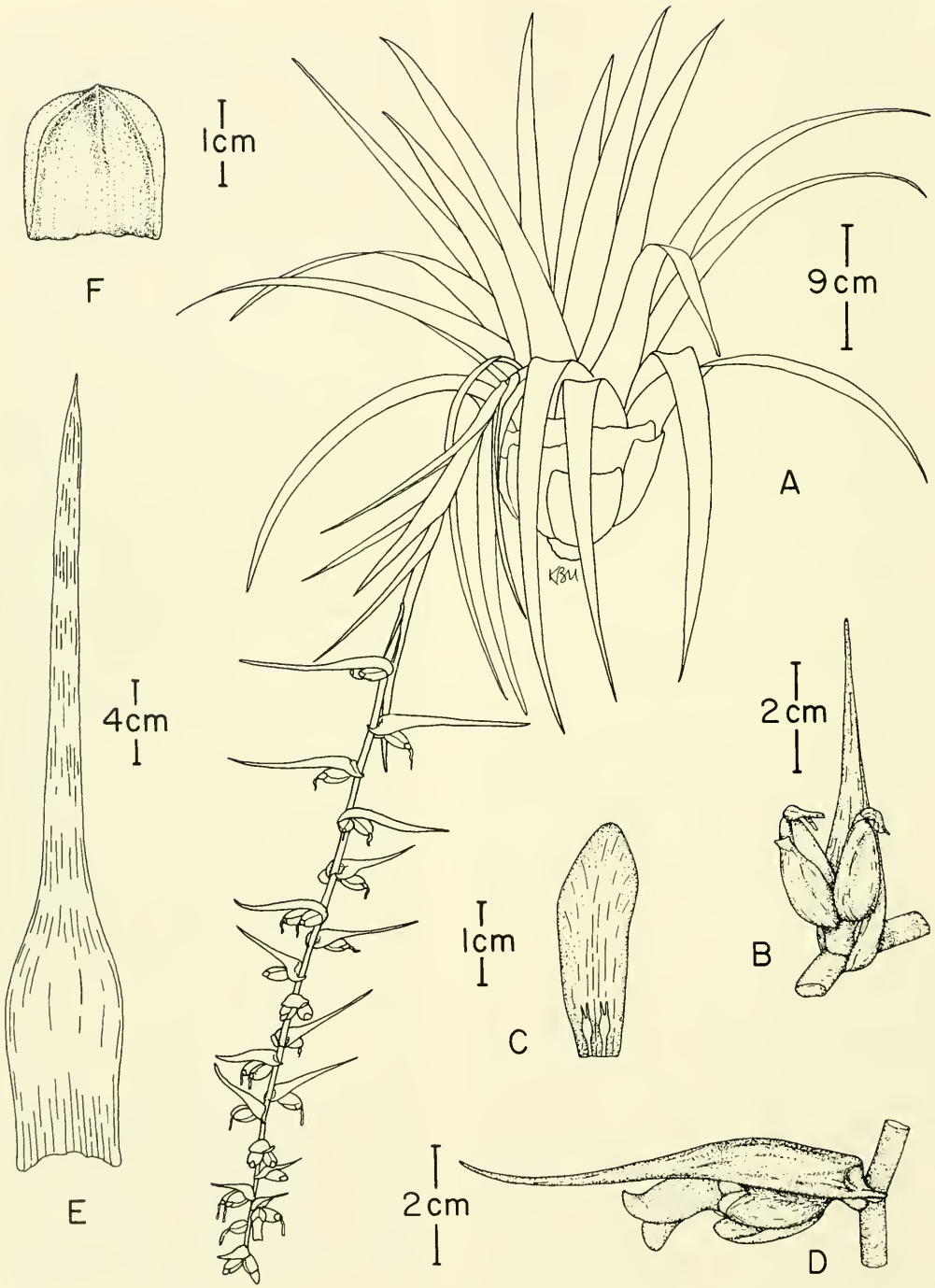


Fig. 22. *Vriesea vietoris*. A. Habit; B. Lateral inflorescence branch; C. Petal; D. Lateral inflorescence branch; E. leaf; F. floral bract excised and flattened. A, B, E, from *(Utley & Utley 2172)*; C, F, from *(Utley & Utley 4784)*; D, from *(Utley & Utley 2216)*.

are diurnal, greenish-white, tubular and weakly zygomorphic. *Vriesea vietoris* is very similar in general appearance to both *V. leucophylla* and *V. hainesiorum* but differs from them in characters mentioned above in the accompanying key, as well as in ecological preference. It is known only from the premontane wet forest, whereas *V. leucophylla* and *V. hainesiorum* are most abundant in the premontane rainforest and premontane moist forest respectively of the Holdridge life zone system (Holdridge, 1967). In the topographically complex region south of Cartago, where these three life zones are closely adjacent, the taxa occur sympatrically. The only indication of potential introgression in the area is the reduction of banding in the leaves of *V. leucophylla*; however the other characters which distinguish the three species remain constant. This paucity of intermediates may be partially explained by the phenologies of the species in the zone of sympatry. *Vriesea vietoris* has been observed in flower during April and early May, while in the same areas *V. leucophylla* displays a flowering peak in July and August. This is in contrast to the strong June flowering peak of the latter species in areas of nonsympatry. *Vriesea hainesiorum,* which is rare in the area of sympatry, typically flowers from May through July. However, despite a deliberate search, flowering specimens of *V. hainesiorum* were not observed in the contact area during the flowering period of *V. vietoris* or *V. leucophylla.*

ADDITIONAL SPECIMENS EXAMINED: COSTA RICA: BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: 18 miles S of Cartago on Interamerican Highway, N side of Talamanca Mts., 5 August 1962, *A. Lee & Bruce L. Haines 763* (US). Near the junction of C. R. Hwy. 2 (Interamerican Highway) and 222 about 4-5 km S of El Empalme in the Cordillera de Talamanca, 16 April 1975, *Utley & Utley 2172* (NOLS), *2173* (DUKE); pasture along the Interamerican Highway 200 yards SE of Casa Mata, 9 May 1976, *Utley & Utley 4744* (CAS), *4745* (NY), *4746* (US), *4748* (DUKE), *4757* (CR) & *4758* (NOLS); along Interamerican Highway W of Cartago, 9 May 1976, *Utley & Utley 4782* (US), *4783* (MO), *4784* (DUKE); along Interamerican Highway S of Cartago, 3 April 1979, *A. Meerow, L. Besse & K. Tan 1117* (SEL). SAN JOSÉ PROVINCE: on C.R. Hwy. 222 about 2 km from the junction with the Interamerican Highway and about 3.5 km E of San Cristóbal Sur, 17 April 1975, *Utley & Utley 2215* (F), *2216* (DUKE); along C.R. Hwy. 12, 6 km from the junction with the Interamerican Highway, 15 April 1976, *Utley & Utley 4648* (F).

17. *Vriesea uxoris* Utley, Brittonia 33:583-584. 1982. Fig. 23

TYPE: COSTA RICA: BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: bog and surrounding thickets about 15.9 km S of El Empalme on the Interamerican Highway, 4 July 1976, *Wilbur 19892* (HOLOTYPE: DUKE!; photographs CR, US).

Epiphytic, acaulescent. LEAVES in a subspreading to subascending rosette, 33.0-44.0 (48.0) cm long; *blades* (18.0) 20.0-24.0 (36.0) cm long and 3.6-5.0 cm wide, green or green suffused with maroon to entirely maroon, ligulate to broadly triangular, apex acute to acuminate; *sheaths* (12.0) 15.0-17.0 (19.5) cm long and 6.0-8.4 cm wide, obovate, castaneous usually with a coating of cinereous trichomes. SCAPE decurved, (34.0) 38.0-44.0 cm long and about 0.4 cm in diameter; *bracts* (13.0) 17.0-23.0 (33.0) cm long and 3.0-4.2 cm wide, the blade and sheath portions not well delineated, ascending to erect becoming divergent or spreading near apices, enfolding the scape in the sheath area, usually red-pink, at times suffused with green or rarely entirely green, ligulate to subligulate or

broadly triangular, apex acute. INFLORESCENCE pendent, 21.0-38.0 cm long and about 17.0-30.0 cm in diameter, pyramidal, rachis glabrous occasionally with numerous castaneous punctulae,green to strongly suffused with red or maroon; *primary bracts* spreading, 11.0-15.0 (21.0) cm long and 2.8-3.6 cm wide, pink to peach or salmon colored, occasionally with fine longitudinal maroon lines, subligulate to broadly triangular, apex acute to acuminate. LATERAL-BRANCHES spreading (0.9) 1.2-1.7 cm long, collaterally 2-flowered, peduncles 0.9-1.4 cm long, rachis 0.0-1.3 cm long. FLOWERS 0.3-0.8 cm pedicellate; *floral bracts* 1.0-1.4 cm long and 1.2-1.7 cm wide, green or yellow-green, drying to brown, even to obscurely nerved, frequently rugulose especially in distal portion, keeled, obovate to suborbicular, apex rounded or truncate, minutely apiculate or torn-incised; *sepals* 2.2-3.0 cm long and 1.0-1.5 cm wide, green drying to pale brown with a castaneous base, coriaceous, obovate, the apex rounded to truncate, occasionally minutely apiculate or torn-incised; *petals* 3.0-3.1 cm long and 0.8-0.9 cm wide, green, obovate; *appendages* 0.6 cm long and 0.2 cm wide; *stamens* in a hood configuration over the style, filaments 1.6-1.8 cm long, anthers 0.4-0.5 cm long; *ovary* 0.4 cm long and 0.3 cm in diameter, style 2.3 cm long; *capsules* 3.8-4.0 cm long and about 0.8 cm in diameter, broadly fusiform, castaneous.

PHENOLOGY: Flowering April and May.

DISTRIBUTION AND HABITAT: Known only from the Cordillera de Talamanca in Costa Rica in the montane rain forest life zone.

DISCUSSION: *Vriesea uxoris* is a distinctive montane species characterized by green to maroon, unmarked leaves, a lax, pendent inflorescence with a comparatively slender rachis and peach or salmon-colored primary bracts. These characters in conjunction with the long sepals (2.2-3 cm) and floral bracts (1.1-1.4 cm) consistently much shorter than them immediately separate *V. uxoris* from the remainder of the thecophylloid vrieseas. *Vriesea uxoris* resembles *V. leucophylla, V. vietoris* and *V. hainesiorum* in its pendent inflorescence, brightly colored primary bracts and green, diurnal flowers. However there are numerous differences in leaf shape, inflorescence and floral characters, and habitat preference. The leaf blades of *V. leucophylla, V. vietoris* and *V. hainesiorum* are narrower (1-3 cm) and generally triangular in outline, Moreover, in the latter three taxa the floral bracts are equal or subequal to the sepals at anthesis and the primary bracts are pink to red in color while the floral bracts of *V. uxoris* are not more than one-half as long as the sepals and the primary bracts are peach to salmon in color. The montane rainforest habitat of *V. uxoris* contrasts with the lower and frequently drier pre-montane habitats of the other pendent-inflorescenced taxa. *Vriesea uxoris* does not occur sympatrically with these species.

SPECIMENS EXAMINED: COSTA RICA: BORDER OF SAN JOSÉ AND CARTAGO PROVINCE: about 17 km SE of El Empalme on the Interamerican Highway, 6 April 1974, *Utley & Utley 811* (CR), *812* (MO) & *843* (DUKE); 17 March 1975, *Utley & Utley 2004* (NOLS), *2005*(DUKE), *2006* (NOLS); 27 October 1975, *Utley & Utley 3202* (CAS); 9 May 1976, *Utley & Utley 4755* (US), *4756*(F).

18. *Vriesea picta*(Mez & Werckle) L. B. Smith & Pitt. Journ. Wash. Acad. Sci 43: 403. 1953.

Thecophyllum pictum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 874. 1904.

TYPE: COSTA RICA: Province not given, near Desengano, elevation 1460 m, *Werckle Bromel. Costaric. 119 pro*

parte. (LECTOTYPE: B!; ISOLECTOTYPE: B!).

Epiphytic, acaulescent to several cm caulescent. LEAVES in a subascending rosette, 33.0-45.0 cm long; *blades* 18.5-30.0 cm long and 3.3-4.8 cm wide, green with darker green wavy transverse lines, these weakly suffused with maroon at the blade-sheath junction, ligulate, apex acute; *sheaths* 12.8-17.6 cm long and 5.0-7.5 cm wide, castaneous abaxially becoming green suffused with indistinct wavy maroon transverse lines distally, brown abaxially with distinct wavy maroon transverse lines, ovate. SCAPE erect, 41.5-61.5

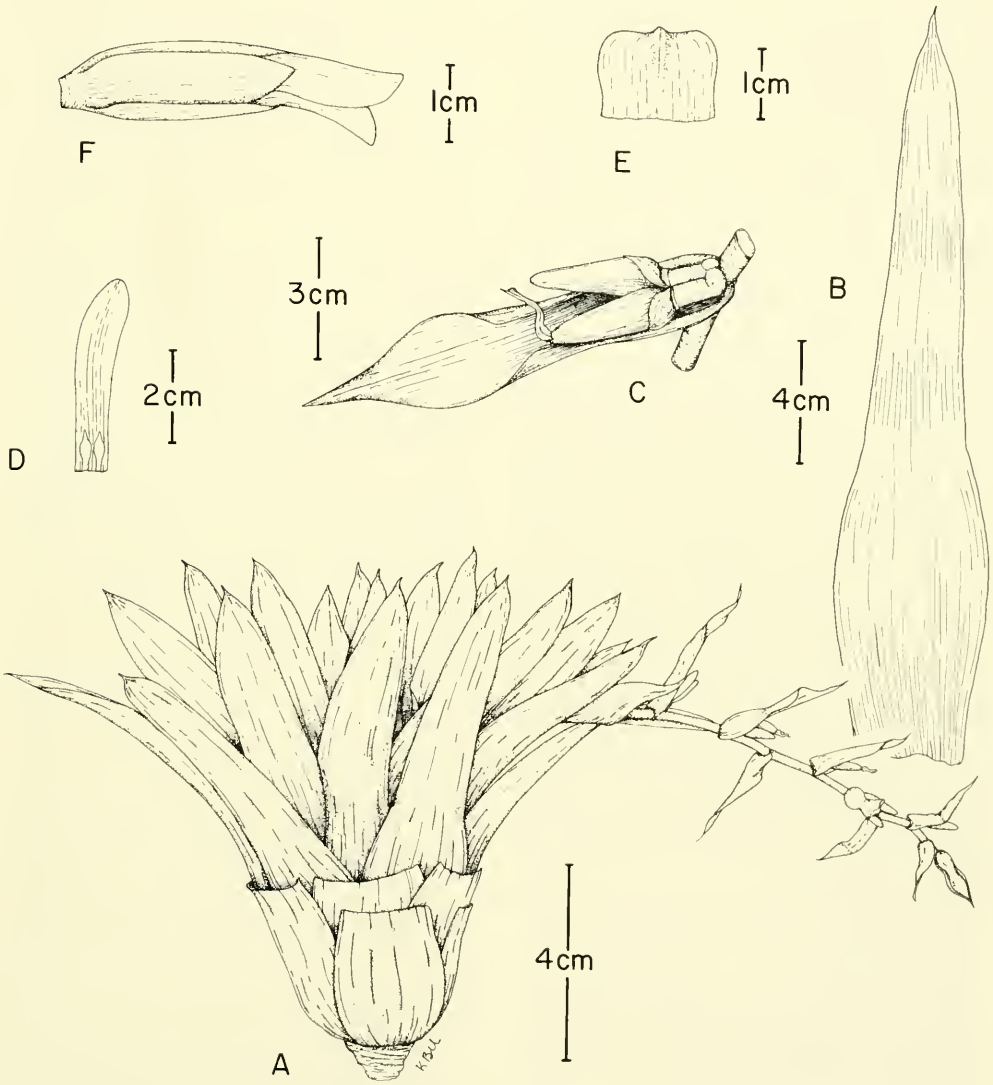


Fig. 23. *Vriesea uxoris.* A. Habit; B. Leaf; C. Lateral inflorescence branch; D. Petal; E. Floral bract, excised and flattened; F. Flower. A, B, C, E, From *(Utley & Utley 4756)*; D, F, From *Wilbur 19892.*

cm long and 0.7-1.0 cm in diameter; *bracts* 6.9-11.0 cm long, blade 3.7-7.7 cm long and 1.8-2.9 cm wide, green with wavy maroon transverse lines, erect, divergent distally, ligulate to subtriangular, apex acute, sheaths about 3.1-3.3 cm long and 3.5-4.5 cm wide, green with faint wavy transverse lines distally, sheathing erect, ovate. INFLORESCENCE erect, 13.0-20.0 cm long and 6.0-11.0 cm in diameter, cylindric; *primary bracts* 6.8-7.8 cm long, blades about 4.0-5.0 cm long and 2.0 cm wide, green with darker green wavy transverse lines, these occasionally suffused with maroon distally, spreading, subligulate, apex acute, sheaths about 3.5 cm long and 4.5 cm wide, ovate in outline. LATERAL BRANCHES spreading to ascending, to 4.5 cm long, collaterally biflowered, pedicels wanting or to 0.1 cm long. FLOWERS sessile; *floral bracts* about 1.6 cm long and 0.5-0.6 cm wide pale green, membranaceous, unkeeled, brown-centered lepidote adaxially, glabrous with brown-margined pellucid punctulae abaxially, lanceolate, apex narrowly acute; *sepals* 1.9-2.2 cm long and 1.3-1.6 cm wide, green suffused with maroon near margins and apex, brown-centered lepidote adaxially immersed lepidote abaxially, elliptic to oblong elliptic, apex acute to obtuse; *petals* 4.5-5.0 cm long and 1.6-1.9 cm wide, greenish white, indistinctly ovate proximally becoming ligulate distally; *appendages* 0.5 cm long and 0.3-0.4 cm wide; *stamens* in a hood configuration over the gynoecium, filaments 4.3-4.5 cm long, anthers 0.6-0.7 cm long; *ovary* more or less 0.6 cm long 0.5-0.6 cm in diameter, style about 4.2 cm long.

PHENOLOGY: Flowering plants collected during May.

DISTRIBUTION AND HABITAT: Known from the type location in Costa Rica and from northwestern Panamá between 1900 and 2000 m in the lower montane rain forest life zone.

DISCUSSION: The type material of *Vriesea picta* must be considered a mixed collection composed of two taxa, *V. picta* and *V. viridis*. However, the element which represents *V. viridis* does not agree with either the diagnosis of *V. picta* or the illustration of *V. picta* in Das Pflanzenreich (Mez, 1934-1935). Specimens of the remaining element, however, agree in all critical characters with both the description and illustration of *V. picta*. This situation possibly originated sometime after the original circumscription of *V. picta*, since the discordant element lacks one of Werckle's original tags identifying it as "119". The addition may have occurred when Mez's personal collection was accessioned into the Berlin Herbarium.

From the scant material of *V. picta* available, this species may be recognized by its caulescent habit, its formation of tank-roots, and its castaneous, brittle leaf sheaths. Flowers of *V. picta* are green-white, strongly zygomorphic and nocturnal. *Vriesea picta* is most similar to *V. stenophylla* and *V. williamsii* in floral morphology, the formation of tank-roots and brittle leaf bases. A combination of features may be used to distinguish these three taxa from one another and include leaf markings, inflorescence length, floral bract shape and length and flower size.

In Costa Rica *V. picta* is still only known from the type location where I re-collected it. Only three flowering individuals were observed (*Utley & Utley 4961, 4979, & 4984*) and these were all part of a large cluster growing in a mass on a tree trunk. No other plants of *V. picta* were seen in the area. The Panamanian material of this taxon is unique in that the floral bracts are absent. This condition has not been noticed in any other specimen of thecophylloid vriesea. Further field study and collections are needed to critically evaluate the status and relationships of this unusual taxon.

SPECIMENS EXAMINED: COSTA RICA: HEREDIA PROVINCE: About 3 km south of the junction of highways 9 and 120 on Highway 9, slopes above the Río

Desengano, 22 May 1976, *Utley & Utley 4961* (DUKE) *4979*(CR) & *4984* (NOLS). PANAMÁ: CHIRIQUÍ PROVINCE: Las Nubes, 7 August 1974, *Croat 26448* (MO) & *26468* (MO).

19. *Vriesea stenophylla*(Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci 43: 403. 1953.

> *Thecophyllum stenophyllum* Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 875. 1904.
> TYPE: COSTA RICA: location not given, *Werckle Bromel. Costaric. n. 112* (HOLOTYPE: B!, photograph US).

Epiphytic, or terrestrial, short caulescent. LEAVES in a ascending or subascending rosette, (15.0) 22.0-36.0 (44.0) cm long; *blades* (9.0) 16.0-28.0 (37.0) cm long and 1.3-2.4 cm wide, green with distinct maroon longitudinal lines, long triangular to ligulate, apex attenuate to acute; *sheaths* (5.6) 6.6-8.6 cm long and 2.0-3.4 cm wide, castaneous abaxially, suffused with maroon longitudinal lines distally and adaxially elliptic to ovate in outline. SCAPE erect, (16.0) 23.0-39.0 cm long and 0.2-0.4 cm in diameter; *bracts* 4.-12.0 (20.0) cm long, blades 2.0-17.0 cm long and 0.7-1.3 cm wide, green with maroon longitudinal lines, erect, divergent distally, ligulate to triangular, apex attenuate or rarely acute, sheaths 1.6-2.3 (2.9) cm long and 1.4-1.7 cm wide, green with longitudinal lines, sheathing erect, ovate. INFLORESCENCE erect, 3.5-6.0 cm long and about 4.0-6.0 cm in diameter, laxly short cylindric rachis green or green with longitudinal maroon lines; *primary bracts* 3.3-5.7 cm long, blades 1.9-3.6 cm long and 0.3-0.9 cm wide, green or green suffused with maroon, marked with distinct maroon longitudinal lines, spreading, subligulate to triangular or long triangular, apex attenuate to narrowly acute, sheaths 1.9-2.2 cm long and 1.0-1.8 cm wide, green with longitudinal maroon lines, ovate to elliptic; LATERAL BRANCHES spreading sessile, the two flowers borne collaterally in the axil of the primary bracts. FLOWERS sessile to rarely 0.3 cm pedicellate; *floral bracts* 0.7-0.9 cm long and 0.4-0.7 cm wide, green or green slightly suffused with maroon, membranaceous, minutely brown lepidote adaxially, glabrous to pellucid punctate and/or immersed lepidote abaxially, ovate, oblongovate or cuniform, apex acute to broadly obtuse or rounded; *sepals* 1.2-1.6 cm long and 0.7-1.0 cm wide, green or green suffused with maroon or castaneous, coriaceous, lepidote adaxially, glabrous abaxially, ovate to elliptic or slightly oblong, apex obtuse to rounded; *petals* 2.4-2.6 cm long and 1.2-1.3 cm wide, white or greenish white, obovate; *appendages* 0.3-0.4 cm long and 0.15-0.3 cm wide; *stamens* in a hood over the gynoecium but only weakly if at all connivent by the anther margins, filaments 1.9-2.0 cm long, anthers 0.3 cm long; *ovary* 0.4 cm long and 0.3 cm in diameter, style 1.6-1.7 cm long; *capsules* about 2.6 cm long and 0.6 cm in diameter, castaneous, fusiform.

PHENOLOGY: Flowering specimens have been collected in January, March and May.

DISTRIBUTION AND HABITAT: Endemic to Costa Rica between 900-1700 m in the premontane rain forest life zone.

DISCUSSION: *Vriesea stenophylla* is a small, relatively inconspicuous species which is infrequent in the premontane rain forests. The leaves of this species usually form an ascending rosette and have comparatively broad longitudinal lines. Its inflorescences are few flowered, bearing greenish white nocturnal flowers with subtubular to zygomorphic corollas.

Based on its caulescent habit, tendency to form tank-roots, longitudinally lined leaves with castaneous, brittle sheaths and more or less open inflorescence with greenish white, frequently zygomorphic corollas, this species

is most closely allied with *V. williamsii* and *V. picta*. *Vriesea stenophylla* is easily separated from these species by a combination of floral bract, sepal and petal length, as well as the length of both the scape and inflorescence and the number of flowers per inflorescence. Although *V. stenophylla* and *V. attenuata* are very distinctive taxa they were difficult to separate from each other using technical characters of leaf markings and floral bract length (Smith and Downs, 1977). This situation is discussed in greater detail under *V. attenuata*.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: north of San Ramón, between Los Angeles Norte and 12 km north of La Balsa or 10-23 km north of San Ramón, 15 December 1974, *Utley & Utley 1634* (DUKE); 8 August 1975, *Utley & Utley 2788* (US), *2813* (DUKE); 27 January 1976, *Utley & Utley 3758* (CR, DUKE, NOLS) & *3793* (MO). CARTAGO PROVINCE: Tapantí Hydroelectric Project, slopes overlooking the Río Grande de Orosi about 4 km beyond the guard house at entrance, 22 March 1976, *Utley & Utley 4371* (F) & *4372* (DUKE); 25 June 1976 *Utley & Utley 5167* (DUKE); between Tausito and Selva, 4-6 km northeast of the Río Grande de Orosí at Tapantí, 27 May 1976, *Utley & Utley 5064* (DUKE) & *5066* (CR). SAN JOSÉ PROVINCE: Alto de La Palma north of San Jerónimo, 19 June 1975, *Utley & Utley 2563* (DUKE); 18 August 1975, *Utley & Utley 2909* (DUKE).

20. *Vriesea williamsii* L. B. Smith, Phytologia 6: 193. 1958. Fig. 12.

TYPE: COSTA RICA. Province of Cartago, on trees in cloud forest near "El Jardin," Cerro de La Muerte, Cordillera de Talamanca, elev. 2700 m, 20 May 1956, *Louis O. Williams 20240a* (HOLOTYPE: US!).

Vriesea sarcolepis L. B. Smith, Phytologia 28: 328. 1974.

TYPE: COSTA RICA: Province of Alajuela, terrestrial, wet montane forest, Volcán Poas, elev. 2525 m, 13 August 1964, *M. F. Tessene 1580* (HOLOTYPE: WIS!, photograph and fragment US!).

Epiphytic or terrestrial, acaulescent to 15.0 cm or, when terrestrial, rarely to 75.0 cm caulescent. LEAVES in an ascending rosette, (20.0) 26.0-36.0 (41.0) cm long, usually with tank-roots in the axils of older leaves; *blades* (11.5) 15.0-24.0 (28.0) cm long and 1.9-3.1 (3.8) cm wide, green occasionally suffused with maroon at times glaucous abaxially, usually with fine maroon, to purple longitudinal lines, these frequently most conspicuous proximally, occasionally with wavy green, maroon or purple wavy transverse markings, ligulate to subligulate or long triangular, apex acute to acuminate or attenuate; *sheaths* (7.0) 9.0-13.0 (15.5) cm long and 3.8-6.4 cm wide, castaneous abaxially, usually with longitudinally purple to maroon lines and/or wavy purple to maroon transverse lines, pale brown adaxially, frequently with purple to maroon longitudinal lines and/or wavy transverse lines, elliptic to ovate. SCAPE 29.0-60.0 (108.0) cm long, erect or curved-erect, 0.3-0.6 cm in diameter; *bracts* 4.0-10.0 (14.5) cm long erect, usually divergent distally, rarely spreading to recurved at tips, blades 2.0-7.0 (11.0) cm long and 0.9-2.1 cm wide, green frequently with fine, maroon or purple, longitudinal lines and/or maroon or purple wavy transverse bands, ligulate or subligulate to triangular or long triangular, apex acute to acuminate, sheaths 1.4-3.4 (5.4) cm long and 1.5-3.2 cm wide, green, frequently with maroon to purple longitudinal lines, sheathing erect, ovate. INFLORESCENCE erect, (6.0) 7.5-15.0 (18.0) cm long and about 5.0-8.9 cm in diameter, cylindric, usually lax, rachis green to brownish red or maroon, glabrous; *primary bracts* 3.5-8.5 cm long, blades 1.3-5.1 cm

long and 0.6-1.8 cm wide, green frequently suffused with maroon and with maroon longitudinal lines and/or wavy transverse lines, spreading, frequently reflexed or recurved at the blade-sheath junction, triangular to subligulate or ligulate, apex acute to acuminate or rarely attenuate, sheaths 1.9-3.5 cm long and 1.8-3.5 cm wide, green frequently with maroon longitudinal lines, ovate to broadly ovate in outline. LATERAL BRANCHES sessile, 2-flowered, these borne collaterally in the axils of the primary bracts. FLOWERS 0.1-0.8 cm pedicellate; *floral bracts* (0.5) 0.7-1.4 cm long and 0.4-1.1 cm wide, green, frequently suffused with maroon, at times strongly so, membranaceous, finely nerved, glabrous to scattered pellucid punctate abaxially and obscurely lepidote adaxially, usually unkeeled or rarely weakly keeled, ovate, oblong or cuniform, frequently asymmetric, apex obtuse or rounded to acute; *sepals* 1.5-2.3 cm long and 0.8-1.4 cm wide, green or green suffused with maroon marginally and distally to entirely maroon or castaneous, coriaceous to subcoriaceous and pliable, unkeeled, lepidote adaxially, glabrous abaxially, elliptic to oblong-elliptic or elliptic-obovate, apex rounded to obtuse or broadly acute; *petals* (3.6) 4.0-4.8 (5.2) cm long and (0.9) 1.4-1.8 cm wide, white or faint greenish white, obovate to oblong-obovate, frequently falcate or subpandurate; *appendages* 0.3-0.4 cm long and 0.15-0.3 cm wide; *stamens* weakly or not at all marginally connivent by the anthers, filaments 2.4-4.4 cm long, anthers (0.3) 0.6-0.8 cm long; *ovary* 0.3-0.6 cm long and 0.3-0.4 cm in diameter, style 3.5-4.8 cm long; *capsule* 2.2-2.3 cm long and 0.6-0.9 cm in diameter, castaneous, fusiform.

PHENOLOGY: Flowering specimens have been collected in March and May.

DISTRIBUTION AND HABITAT: Known from Costa Rica between 1900-2800 m in the lower montane and premontane rain forest life zones and extending slightly into the montane rain forest life zone.

DISCUSSION: *Vriesea williamsii* is characterized by its branching caulescent habit and by the production of tank-roots in the axils of the older leaves. The erect, laxly flowered inflorescences of this species produce white, strongly zygomorphic nocturnal flowers. On several occasions *V. williamsii* was encountered growing terrestrially in a montane bog in the Cordillera de Talamanca. These particular plants were very long caulescent (1 m or longer); this condition has not been found in any other population of *V. williamsii*.

Vriesea williamsii and *V. sarcolepis* represent the extremes of a geographical and morphological continuum. Specimens from the Cordillera de Talamanca often have leaves which are long triangular with fine maroon longitudinal lines, whereas plants from the upper slopes of Volcan Poas and Volcán Barba have subligulate leaves suffused with maroon wavy crossbands. The extreme representations of this combination of characters results in individuals which vegetatively are very distinct from each other. This is reflected in the type specimens of both taxa, which at first glance appear remarkably different. At geographically intermediate collecting sites, this striking character combination breaks down. Many collections of *V. williamsii* from the Cordillera de Talamanca have subligulate leaves, but none have wavy crossbands either in place of, or in addition to the fine longitudinal lines characteristic of the type of *V. williamsii*. Several specimens from the north side of Volcán Barba in the Cordillera Central have both wavy crossbands as well as fine maroon longitudinal lines. Individuals from the vicinity of Vara Blanca and lower elevations in the Cordillera de Talamanca have entirely green leaves or are marked obscurely at the sheath-blade junction. Moreover, some collections from the type locality of *V. sarcolepis* on the slopes of Volcán Poas have both maroon wavy crossbands and longitudinal lines (*Utley & Utley 4727 A*) or only longi-

tudinal lines (*Utley & Utley 1922*). Inflorescence and floral characters of all plants that I was able to observe were essentially identical, varying only slightly in size. In light of the variability of vegetative characters which have been used to separate these taxa, *V. sarcolepis* cannot be maintained as a distinct species, and I am also reluctant to recognize it as a variety or subspecies of *V. williamsii*.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: Volcán Poas, 25 May 1937, *Valero 1711* (F), 13 August 1964, *Lent 191* (CR); between the junction of highways 9 and 120 and the summit of Volcán Poas, 11 March 1975, *Utley & Utley 1922* (DUKE) & *1948* (US); 2 km south of the entrance to Parque Nacional Volcán Poas, 3 May 1976, *Utley & Utley 4727 A, B & C* (DUKE, NOLS, CR). BORDER OF ALAJUELA AND HEREDIA PROVINCES: on the finca of Mike (Miguel) Canon near the junction of highways 9 and 120, 20 July 1975, *Utley & Utley 2665 A,B,C&D* (DUKE, MO, GH, F). CARTAGO PROVINCE: Tapantí Hydroelectric Project between 9 and 14 km southeast of Orosí, slopes above the Río Grande de Orosí, 13 December 1974, *Utley & Utley 1611* (DUKE) & *1627* (NOLS); 22 March 1976, *Utley & Utley 4356* (NY) & *4364* (DUKE). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: in and around a mountain bog 17 km southeast of El Empalme on the Interamerican Highway, 28 December 1973, *Utley & Utley 545* (DUKE), *565* (US), *566* (DUKE); 6 April 1974, *Utley & Utley 806* (US), *807* (CR), *808* (DUKE), *810A* (DUKE); bog 1 km south of El Empalme, 17 December 1974, *Utley & Utley 1718* (DUKE); near the junction of highways 2 and 222 about 5 km north of El Empalme, 16 April 1975, *Utley & Utley 2181 A, B & C* (DUKE, NOLS, MICH); about 17 km south of El Empalme on the Interamerican Highway, 3 August 1975, *Utley & Utley 2731* (DUKE) *2732* (US), *2733* (CR), *2734* (F), *2735* (MO), *2738* (K) & *2739* (DUKE). HEREDIA PROVINCE: between Sacremento and 1 km beyond Laguna Barba at the summit of Volcán Barba, 12 April 1975, *Utley & Utley 2029 A&B* (DUKE) & *2045* (CR); 1 May 1975, *Utley & Utley 2314* (DUKE); 25 January 1976, *Utley & Utley 3707* (DUKE), *3720* (BM), *3721* (US), *3722* (F), *3723 A&B* (MO, NOLS), & *3724* (DUKE); 2-3 km southeast of the junction of highways 9 and 120 on Highway 9, slopes over the Río Desengano, 27 March 1976, *Utley & Utley 4376* (GH), *4328* (MO) & *4386* (DUKE); 22 May 1976, *Utley & Utley 4963* (NY) & *4964* (DUKE). SAN JOSÉ PROVINCE: Hwy. 4, 3-4 km south of Aserrí in the Cedral, 9 June 1974, *Utley & Utley 925* (DUKE); the Cedral (Cerros de Escazú), summit of Cerro Daser, 30 April 1975, *Utley & Utley 2508* (US), *2509* (CR) & *2510* (F).

21. *Vriesea attenuata* L. B. Smith & Pitt. J. Wash. Acad. Sci 43: 401. 1953.

Thecophyllum acuminatum L.B. Smith, Contr. Gray Herb. 117: 30. 1973, not *Vriesea acuminata* Mez & Werckle in Mez, 1904.

TYPE: COSTA RICA: SAN JOSÉ PROVINCE: on tree, La Palma, elev. ca. 1600 m, *Standley 38276*. (HOLOTYPE: US!).

Epiphytic or terrestrial, to 12 cm caulescent. LEAVES in an ascending to subspreading rosette, 11.0-16.5 cm long; *blades* 6.0-10.5 cm long and 1.4-2.0 cm wide, green, usually cinerous abaxially, occasionally with fine purple longitudinal lines proximally, subligulate to triangular, apex narrowly acute to attenuate; *sheaths* 4.0-5.8 cm long and 2.5-3.8 cm wide, castaneous abaxially pale brown or grey-brown adaxially, elliptic. SCAPE erect, 18.4-30.5 cm long and about 0.2-0.4 cm diameter; *bracts* 4.1-8.1 cm long, blades 1.6-5.3 cm long and 0.9-1.5 cm wide,

green frequently cinereous, erect to divergent distally, subligulate to triangular, apex narrowly acute to attenuate, sheaths 2.2-3.7 cm long and 1.1-2.1 cm wide, sheathing-erect, elliptic to ovate. INFLORESCENCE erect, 3.0-6.0 cm long and 4.0-7.0 cm in diameter, short, dense cylindric; *primary bracts* 3.5-4.7 cm long, blades 1.8-2.4 cm long and about 1.0-1.3 cm wide, spreading, triangular, apex narrowly acute to attenuate, sheaths 1.5-2.7 cm long and 1.2-2.9 cm wide, ovate to broadly elliptic or suborbicular. LATERAL BRANCHES ascending to subspreading, 2.0-3.0 cm long, collaterally biflowered, peduncle 0.0-0.3 cm long, rachis 0.0-1.2 cm long FLOWERS sessile to 0.3 cm pedicellate; *floral bracts* 1.1-1.4 cm long and 1.0-1.5 cm wide, green, submembranous to coriaceous, brown-centered lepidote adaxially, immersed brown-centered lepidote with brown-margined pellucid excrescences abaxially, unkeeled or infrequently keeled, broadly obovate, oblong-obovate to elliptic or suborbicular, apex obtuse to broadly rounded or suborbicular, usually minutely acuminate; *sepals* 1.1-1.6 cm long and 0.8-1.2 cm wide, green, coriaceous, brown-centered lepidote adaxially and immersed brown-centered lepidote abaxially, obovate to elliptic, apex obtuse to broadly rounded; *capsules* about 2.0 cm long and 0.7-1.9 cm in diameter, fusiform dark brown to castaneous in color.

PHENOLOGY: Although flowering specimens have been collected only during August, this species probably flowers throughout the late dry season and early rainy season (June-September).

DISTRIBUTION AND HABITAT: Costa Rica and Panamá between 700-1600 m in the premontane rain forest life zone and possibly extending into the premontane basal belt transition of the tropical wet forest life zone.

DISCUSSION: *Vriesea attenuata* is an infrequent species distinguished by the cinereous abaxial surfaces of the leaf blades and the dark castaneous sheaths in conjunction with the floral bracts which are about equal to to shorter than the sepals. The flowers are white and nocturnal. Although the exact form of the corolla is not known, the general shape is probably tubular to narrowly campanulate.

Vriesea attenuata is most closely related to and frequently grows sympatrically with *V. comata* and is difficult to distinguish from this taxon in vegetative condition. In flower or fruit, they are readily separable from each other. In contrast to the 2.5-3.0 cm long, obovate, olive-green to brown capsules characteristic of *V. comata*, those of *V. attenuata*, are shorter (about 2 cm fusiform and castaneous, these species may also be separated by the degree of development of the sterile coma and floral bract length. Although only a few flowering specimens have collected of *V. attenuata,* this taxon appears to lack the gelatinous matrix on its inflorescences which is commonly observed in *V. comata. Vriesea attenuata* also superficially resembles *V. kathyae*, from which it differs in sepal length, leaf length and coloration and floral bract length.

Smith and Downs (1977) placed *V. attenuata* in synonymy with *V. stenophylla* on the basis of the congruence of the taxa in floral bract length relative to sepal length and the presence of longitudinal lines in the leaves of both taxa. After an evaluation of the type material and my personal collections in conjunction with my field observations, I am unable to agree with their disposition of this taxon. *Vriesea attenuata* can be separated from *V. stenophylla* consistently on the basis of its longer floral bracts (1.1-1.4 cm vs. 0.7-0.9 cm) and its cinereous abaxial leaf surfaces. Although the inflorescences of these taxa appear similar, they are subtly different in form. Moreover, the longitudinal lines which are present in the leaves of *V. attenuata* are narrow and the color is confined to the veins, while those of *V. stenophylla* are much broader and the color is not

confined to the veins.

SPECIMENS EXAMINED: COSTA RICA: PROVINCE OF ALAJUELA: North of San Ramón between Los Angeles Norte and about 7 km north, 15 December 1974, *Utley & Utley 1638* (DUKE); north of San Ramón between La Balsa and about 4.5 km north,26 February 1975, *Utley & Utley 1852* (DUKE), & *1854* (CR); north of San Ramón between La Balsa and the Río Cataratas or about 12 km north of La Balsa, 27 January 1976, *Utley & Utley 3738* (DUKE), *3747* (CR), *3748* (NOLS), *3749* (F), *3759* (NY), *3764* (MO) *3765* (K), *3766* (DUKE), *3749* (US); about 4 km north of la Balsa de San Ramón, 8 February 1976, *Utley & Utley 4115* (DUKE). BORDER OF ALAJUELA AND HEREDIA PROVINCES: Vicinity of Colonia Virgen del Socorro on and around the finca of Sr. Carlos Molina or about 3 to 6 km east of Cariblanco, 10 August 1975, *Utley & Utley 2850* (NOLS) *2860* (US), *2863* (DUKE). SAN JOSÉ PROVINCE: La Hondura, 9 March 1926, *Standley & Valerio 51909* (US). PANAMÁ: COCLE PROVINCE: north of El Valle de Anton, trail to Las Minas, 2 December 1941, *Allen 2884* (US). VERGUAS PROVINCE: northwest of Santa Fe, 8.8 km from Escuela Agricola Alto de Piedra, 25 February 1975, *Mori & Kallunki 4854* (US).

22. *Vriesea comata* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

Thecophyllum comatum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 871. 1904.
TYPE: COSTA RICA: near Turrialba, alt. 900 m, *Werckle s.n.* (HOLOTYPE: B!, photograph US!).

Vriesea hygrometrica var. *angustifolia* L.B. Smith Phytologia 8: 222. 1962.
TYPE: COSTA RICA: without further locality, *Robert G. & Catherine Wilson 32* HOLOTYPE: US!).

Epiphytic or terrestrial, to 10 cm caulescent. LEAVES in a spreading to subascending rosette, 16.0-23.0 (26.0) cm long: *blades* 9.0-14.0 (16.5) cm long and 1.5-3.2 cm wide, green, usually with longitudinal purple-castaneous lines proximally, ligulate to long triangular, apex acute to acuminate or attenuate; *sheaths* 5.0-9.5 cm long and 2.7-4.5 cm wide, castaneous abaxially, occasionally with longitudinal purple-castaneous lines distally, plumbeous adaxially, usually with longitudinal purple-castaneous lines, elliptic to ovate or obscurely obovate. SCAPE erect, (16.0) 19.0-23.0 (25.0) cm long and 0.3-0.5 cm in diameter; *bracts* 4.5-10.0 (14.0) cm long, blades 3.0-6.5 (9.5) cm long and 1.2-2.4 cm wide, green, erect divergent distally, ligulate to subligulate or triangular, apex acute to attenuate, sheaths (1.8) 2.8-4.0 (5.2) cm long and 2.2-3.2 cm wide, green, sheathing erect ovate. INFLORESCENCE erect, 4.5-9.5 cm long and 5.0-10.0 cm in diameter, short, dense cylindric to subcapitate; *primary bracts* 5.0-7.5 cm long, the blade and sheath merging gradually, subligulate to triangular, apex acute to attenuate, sheaths (2.0) 2.6-3.4 cm wide, green ovate. LATERAL BRANCHES spreading to ascending, sessile to 0.3 cm pedicellate, the 2 or rarely 3 flowers borne collaterally or subcollaterally. FLOWERS sessile to 0.2 cm pedicellate; *floral bracts* 2.5-3.0 cm long and 1.7-2.2 (2.7) cm wide, green, subcoriaceous, brown-centered lepidote on both surfaces, strongly keeled, the bracts usually conduplicately folded along the keel, ovate to oblong-ovate, apex broadly acute to rounded, occasionally asymmetric; *sepals* 1.3-1.6 cm long and 0.8-1.0 cm wide, green coriaceous, brown-centered lepidote adaxially, brown-centered, frequently immersed lepidote abaxially elliptic or rarely obovate, apex obtuse to broadly acute, *petals* about 2.5-2.8 cm long and 1.1

cm wide, white; *appendages* 0.2 cm long and 0.15-0.2 cm wide; *stamens* in a hood configuration over the gynoecium, the filaments flexed and the anthers weakly connivent by their lateral margins, filaments about 2.1 cm long and the anthers 0.4 cm long; *ovary* about 0.35 cm long and 0.4 cm in diameter, style 1.7-1.8 cm long; *capsules* 2.2-2.5 cm long and about 0.8 cm in diameter, obovate, olive-green to brown.

PHENOLOGY: A single flowering specimen has been collected in January.

DISTRIBUTION AND HABITAT: Known only from Costa Rica where the species has been collected between 700-1500 m in the premontane rain forest life zone. Considering the abundance of this species at middle elevations in Costa Rica, more intensive collecting in Panama presumably would result in the collection of this taxon.

DISCUSSION: *Vriesea comata* is notable for its subcapitate to short cylindric inflorescence terminated by a conspicuous sterile coma. The flowering inflorescence is usually covered with a gelatinous matrix similar to that observed in *V. capitata* and *V. bracteosa*. As a result, the white, campanulate nocturnal flowers which are borne in the axils of the usually spreading primary bracts emerge from the exudate at anthesis. The spreading rosettes of *V. comata* are relatively small and formed of leaves with castaneous sheaths and green blades which are longitudinally lined with purple proximally. *Vriesea comata* is readily distinguished from other thecophylloid vrieseas in fruit by its obovate, olive-green to brown capsules.

The type of *V. hygrometrica* var. *angustifolia* is very similar in its critical characters to *V. comata*. The taxa were tacitly separated using leaf pubescence (Smith and Downs, 1977). In *V. comata* the leaves were described as cinereously pubescent while those of *V. hygrometrica* var. *angustifolia* were thought to be glabrous or brown-punctulate. However, these taxa share a number of important characters including leaf shape, color, and marking as well as primary bract shape and orientation, inflorescence shape and floral bract length. These features coupled with a striking congruence in overall appearance are compelling reasons for placing *V. hygrometrica* var. *angustifolia* in synonomy under *V. comata*.

Vriesea comata is most closely related to *V. attenuata* with which it is frequently found growing sympatrically. Although few flowering specimens of either taxon have ever been collected, *V. comata* and *V. attenuata* appear to flower at different times of the year. However, more collections of flowering material are needed to verify these observations. Like *V. attenuata, V. comata* also superficially resembles *V. kathyae,* but it is immediately separable from this taxon on the basis of floral bract and sepal length, leaf coloration and capsule characters. The species relationships of these three taxa are further discussed under *V. attenuata* .

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: Roadside and pasture trees between Hwy. 9 and Laguna Hule on a semi-maintained secondary road, between 0.5 and 5.0 km northwest of Cariblanco, 900-1000 m, 16 October 1974, *Utley & Utley 1370* (CR, DUKE, F, K, NOLS, US); 7 December 1975, *Utley & Utley 3561* (DUKE); North of San Ramón on road to Los Angeles Norte, between Los Angeles Norte and 7 km north 1000-1200 m, 15 December 1974, *Utley & Utley 1680* (DUKE) & *1684* (MO); North of San Ramón between La Balsa and 4.5 km north, 1000 m, 26 February 1975, *Utley & Utley 1854* (DUKE) & *1863* (CR); North of San Ramón between Los Angeles Norte and 7 km north of La Balsa, 900 m, 8 August 1975, *Utley & Utley 2801* (DUKE); North of San Ramón, between La Balsa and the Río Cataratas, 550-1100 m, 27 January 1976, *Utley & Utley 3750* (US), *3770* (F), *3771* (DUKE), *3772*(NOLS), *3773* (CAS), *3790* (NOLS),

3791 (CR), & *3792* (GH); 7 to 9 km north of San Ramón, 1100 m, 27 January 1976, *Utley & Utley 3798* (US), *3800* (DUKE) & *3801* (F); about 13 km north of La Balsa de San Ramón on roadbanks and hillsides above the Río Catartas, 500-600 m, 8 February 1976, *Utley & Utley 4061* (DUKE); about 4 km north of La Balsa de San Ramón, 1000 m, 8 February 1976, *Utley & Utley 4109* (DUKE). BORDER OF ALAJUELA AND HEREDIA PROVINCES: 3-6 km east of Cariblanco in the vicinity of Colonia Virgen del Socorro, 900 m, 10 August 1975, *Utley & Utley 2857* (DUKE) & *2858* (CR). CARTAGO PROVINCE: 19 km south-southeast of the town of Turrialba, in the region southwest of Platanillo, 990-1200 m, 23 July 1975, *Utley & Utley 2684* (US), *2685* (DUKE), *2686*(CR), *2687* (NOLS), *2688* (B), *2689* (MO), *2690* (MICH) & *2691* (GH). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: about 5 km northeast of San Isidro de Heredia on Calle Yerbabuena, 1400 m, 3 April 1976, *Utley & Utley 4474* (DUKE). SAN JOSÉ PROVINCE: Alto de La Palma, Finca Porvenir, in secondary growth and remnant trees and pastures, 1500 m, 18 August 1975, *Utley & Utley 2901* (DUKE); vicinity of Bajo la Hondura, between the plateau and the steel bridge over the Río Hondura, 1050 m, 23 October 1975, *Utley & Utley 3183* (DUKE); about 7 km north of San Jerónimo in the vicinity of La Palma on C.R. Hwy. 220, 1500 m, 27 December 1975, *Utley & Utley 3686* (DUKE).

23. *Vriesea singuliflora* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953.

Thecophyllum singuliflorum Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 870. 1904.

TYPE: COSTA RICA: *Werckle 89* (HOLOTYPE: B!, photograph US!).

Probably epiphytic, slightly caulescent. LEAVES in a ascending rosette, to about 22.0 cm long, drying to brown; *sheaths* abaxially castaneous with pale margins, adaxially light brown. SCAPE erect, about 18.0 cm long, 0.1 cm in diameter or slightly less; *bracts* about 5.5 cm long, blades erect, spreading distally, drying brown with traces of purple, apex acute to attenuate, sheaths clasping-erect, drying brown. INFLORESCENCE erect, 3.0-7.0 cm long and 2.0-3.0 cm in diameter, loosely cylindric; *pirimary bracts* spreading, blades 2.0 cm long and about 0.3 cm wide, dried brown, filiform, apex attenuate, sheaths broadly ovate to suborbicular, 1.0 cm long and 1.0 cm wide. LATERAL BRANCHES spreading, bearing a single, secund flower and a minute vestige of a second flower. FLOWERS with pedicels 0.3-0.4 cm long; *floral bracts* 0.6 cm long and 0.6 cm wide, chartaceous-membranaceous, finely nerved, ecarinate or with an indistinct longitudinal fold near the right margin, broadly elliptic to subrotund, apex broadly obtuse; *sepals* 1.5 cm long and 1.1-1.2 cm wide, coriaceous, broadly elliptic to suborbicular; *petals* 2.0 cm long and 0.7 cm wide, elliptic; *appendages* 0.2-0.3 cm long and 0.15 cm wide; *stamens* probably in a hood configuration over the gynoecium, filaments 1.4 cm long, anthers 0.4 cm long and connivent by their lateral margins into an androecial hood; *ovary* 0.4 cm long and about 0.2 cm wide, style 1.3 cm long, curved and the stigma probably oriented away from the androecial hood.

PHENOLOGY: Unknown, but the type specimen was collected in January and appears to have been flowering or near flowering.

DISTRIBUTION AND HABITAT: Known only from the type location, Carillo, in Costa Rica at 300 m elevation in the tropical wet forest life zone.

DISCUSSION: Although *Vriesea singuliflora* is known only from the type and one

other collection, it is distinct among the thecophylloid vrieseas in consistently having one-flowered lateral branches. From my examination of the material, the flowers appear to be either campanulate or tubular. Although the flowers of this taxon perhaps are diurnal, they are more likely either crepuscular or nocturnal. During my field work, I have never observed diurnal flowering thecophylloid vrieseas at elevations lower than 1500 meters; these taxa appear to be restricted to montane and premontane regions. In contrast, nocturnal flowering taxa are abundant at lower elevations in premontane and lower montane life zones. Although thecophylloid vrieseas have been collected frequently at lower elevations (700-1500 m), *V. singuliflora* is unique among these taxa in apparently growing at low elevations (300 m) in tropical wet forests.

Considering the green, unmarked leaf blades and castaneous leaf sheaths with pale margins that are found in *V. singuliflora* and its ecological preference, this taxon probably has its closest affinities with the *comata* species group. However, this species lacks large floral bracts that are characteristic of several species in the group. Because I was never able to collect *V singuliflora*, I am by no means certain of its exact nature and affinities. Further collections and field observations are needed to resolve the status of this anomalous species.

SPECIMENS EXAMINED: COSTA RICA: PROVINCE OF SAN JOSÉ (?): Vicinity of Carillo, January 1908, *Werckle 144* (=Museo Nacional de Costa Rica #17423, (B).

24. *Vriesea hygrometrica* (Andre) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953. Fig. 13

Caraguata hygrometrica Andre, Enum. Bromel. 6. 13 December 1888.
TYPE: COLOMBIA: NARINO: Alto de San Antonio near Cali, *Andre 2638* (HOLOTYPE: K!, photography US!).
Guzmania hygrometrica (Andre) Andre ex Mez, DC. Monogr. Phan. 9: 919. 1896.

Thecophyllum hygrometricum (Andre) Mez, Bull. Herb. Boiss ser. 11. 3: 131. 1903.

Epiphytic or terrestrial to 8 cm caulescent. LEAVES in a subspreading to ascending rosette, 21.0-31.0 (52.1) cm long; *blades* (13.5) 17.5-21.0 (34.5) cm long and 2.0-3.8 cm wide, green with fine wavy transverse lines, these ranging from dark green and relatively inconspicuous to deep red-maroon, frequently most pronounced proximally, ligulate to subligulate, apex acute to acuminate or rarely attenuate; *sheaths* 7.4-13.5 (17.6) cm long and 3.7-6.2 cm wide, castaneous with pale margins abaxially and grey to greyish-brown adaxially, frequently with wavy transverse lines distally, elliptic to oblong or oblong-ovate. SCAPE erect or curved-erect, 33.5-45.0 (72.7) cm long and 0.4-0.8 cm in diameter; *bracts* (3.1) 3.8-7.6 (9.3) cm long, the blades (1.0) 1.5-3.6 (6.0) cm long and 1.0-1.9 cm wide, green occasionally suffused with wavy transverse lines, erect to divergent apically, triangular to ligulate or subligulate, apex acute to acuminate or attenuate, sheaths 2.1-4.0 cm long and 1.9-3.3 (3.9) cm wide, drying to ochre adaxially sheathing erect, ovate to elliptic in outline. INFLORESCENCE erect, 5.0-6.5 (12.0) cm long and 5.5-7.0 (9.5) cm in diameter; *primary bracts* 3.1-5.8 cm long, blades 1.0-2.8 (3.7) cm long and 1.0-1.7 cm wide, green occasionally with wavy transverse lines, spreading at anthesis, triangular, apex acute to acuminate or attenuate, sheaths 2.1-3.3 cm long and 2.0-3.7 cm wide, ovate or broadly ovate to elliptic. LATERAL BRANCHES spreading or divergent 3.0-4.1 cm long collaterally 2-flowered, peduncle wanting to 0.4 cm long, rachis wanting to 0.1 cm long. FLOWERS sessile; *floral bracts*

(2.1) 2.5-3.3 (3.8) cm long and 1.8-3.0 cm wide, green, subcoriaceous, brown-centered lepidote to subglabrous, keeled, and the bracts usually conduplicate along the keel, oblong to oblong-ovate, apex obtuse to rounded, frequently short acuminate or torn-incised; *sepals* 1.4-2.0 cm long and 0.9-1.3 cm wide, green drying pale castaneous, coriaceous, brown-centered lepidote adaxially, frequently immersed lepidote abaxially, elliptic to obovate, apex obtuse to rounded, frequently minutely apiculate; *petals* about 2.3-3.4 cm long and 1.3-1.8 cm wide, white, elliptic to obovate with a medial constriction on the lateral margins; *appendages* 0.4-0.5 cm long and about 0.2 cm wide; *stamens* in a hood configuration over the style, anthers connivent by their latral margins, filaments 1.9-2.6 cm long, anthers 0.5-0.8 cm long; *ovary* 0.4-0.6 cm long and 0.3-0.4 cm in diameter, style 2.0-2.7 cm long; *capsules* about 1.9 cm long and 0.8 cm in diameter, castaneous.

PHENOLOGY: Flowering plants have been collected in February, April, May and July. Time of flowering apparently is population dependent, and for the species as a whole probably spans several months.

DISTRIBUTION AND HABITAT: This species is the widest ranging thecophylloid, extending from southern Mexicó to Ecuador. The species ranges from 700-1500 m in elevation and is found in the premontane rain forest and lower montane rain forest and possibly extends into the premontane wet forest.

DISCUSSION: Among the thecophylloid vrieseas, *Vriesea hygrometrica* has the most widespread distribution, extending from southern Mexico through Central America and into Ecuador. Considering its distribution, this taxon remains poorly collected outside of Costa Rica. *Vriesea hygrometrica* is a variable species with green leaves that are frequently suffused proximally with wavy transverse lines ranging from green to red-maroon in color. Inflorescences of *V. hygrometrica* are short, dense cylindric to subcapitate at anthesis and frequently elongate during and after anthesis so that fruiting inflorescences are sublaxly cylindric. Moreover, the inflorescences are typically covered with a gelatinous exudate at anthesis. The white to greenish white campanulate flowers are nocturnal. In one collection, *Utley & Utley 877*, the flowers had a sweet, spicy odor in the early evening.

Vriesea hygrometrica is very similar to *V. notata* and , at times, is difficult to distinguish from this latter taxon. The only character that separates these taxa consistently is the presence of longitudinal lines in the leaves, scape bracts and primary bracts of *V. notata* and their absence in *V. hygrometrica*. Populations of *V. notata* from Tapanti region exhibit a pronounced elongation of the inflorescence post anthesis. I doubt that an acyanic individual of *V. notata* in which the inflorescence had elongated post anthesis could be reliably distinguished from *V. hygrometrica*. Further field collections and observations, coupled with a study of breeding systems, are necessary to determine if the current delimitation of these taxa is biologically sound. For the present, I have taken the course which causes the fewest taxonomic changes.

Vriesea hygrometrica and *V. notata* are most similar to *V. kathyae* in habit, habitat and overall appearance. *V. kathyae* is regularly sympatric with these two taxa and may be distinguished from them by its shorter floral bracts, sepals and petals.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: north of San Ramón between Los Angeles Norte and about 7 km north of La Balsa, 26 February 1975, *Utley & Utley 1858* (US) & *1862* (DUKE); shore of Laguna Hule west of Cariblanco, 18 April 1975, *Utley & Utley 2238 A* (DUKE); 8 August 1975, *Utley & Utley 2816* (DUKE); about 5 km west of

Cariblanco on the road to Laguna Hule, 7 December 1975, *Utley & Utley 3564* (DUKE); between La Balsa de San Ramon and the Río Cataratas, 8 February 1976, *Utley & Utley 4062* (DUKE), *4110* (US), *4111* (CR), *4112* (F), *4113* (NOLS), *4114* (DUKE) *4119* (MO) *4127* (K), *4128* (DUKE) & *4131* (NY). BORDER OF ALAJUELA AND PUNTARENAS PROVINCES: evergreen forest and wet wind-gap formations on and near the Continental Divide about 2-5 km east and southeast of Monte Verde, 17-20 March 1973, *Burger & Gentry 8618* (CR, F). CARTAGO PROVINCE:- mountains south of El Muneco, 7 April 1974, *Utley & Utley 877* (DUKE); road from Tapantí to Taus and Tausito, 27 May 1976, *Utley & Utley 5037* (DUKE), & *5039* (NOLS); between Tausito and Selva, 4-6 km northeast of the Río Grande de Orosí at Tapantí; 27 May 1976, *Utley & Utley 5067* (CR), *5068* (US), *5069* (CAS), *5070* (F), *5071* (DUKE), *5072* (GH), & *5073* (DUKE). SAN JOSÉ PROVINCE: Alto de La Palma, 29 June 1974, *Utley & Utley 982 A, B & C* (DUKE, US, CR); 6 July 1975, *Utley & Utley 2573* (DUKE), *2574* (F), *2575* (NOLS), *2589* (MEXU); 18 August 1975, *Utley & Utley 2907 A, B & C* (DUKE, MICH, MO); vicinity of Bajo la Hondura, between the Finca on the plateau and the steel bridge over the Río Hondura, 23 October 1975, *Utley & Utley 3184* (DUKE). MEXICÓ: OAXACA: Vista Hermosa, 50 miles south of Valle Nacional, 28 April 1960, *Van Hyning 6051* (US). PANAMÁ: CHIRIQUÍ PROVINCE: Cerro Colorado, along road above San Felix, 14 July 1976, *Croat 37107* (US).

25. *Vriesea kathyae* Utley, sp. nov. Fig. 24

A *V. hygrometrica* (André) L.B. Smith & Pitt. et *V. notata* L.B. Smith & Pitt., quibus verisimiliter affinis, bracteis florigeris, sepalis et petalis minoribus, laminis foliorum russis differt.

Epiphytic or terrestrial, to about 4.0 cm caulescent. LEAVES in a subspreading to ascending rosette, 17.0-32.0 cm long; *blades* 10.7-22.5 cm long and 1.6-2.0 cm wide, green suffused with pink or russet-brown marginally or abaxially, with fine longitudinal maroon or purple lines, these frequently more pronounced proximally, ligulate, apex attenuate; *sheaths* 7.2-9.3 cm long and 2.6-3.8 cm wide, dark castaneous abaxially frequently with pale margins and fine longitudinal maroon lines distally, pale brown or greyish brown with fine longitudinal maroon lines adaxially. SCAPE erect, 27.0-35.0 cm long and 0.3-0.4 cm in diameter; *bracts* 4.1-7.9 cm long, blades 1.9-5.7 cm long and 0.8-1.8 cm wide, green with maroon longitudinal lines, drying to brown, erect to divergent distally, subligulate to long triangular, apex acute to narrowly acute or attenuate, sheaths 1.9-2.8 cm long and 1.8-2.4 cm wide, sheathing erect, broadly ovate. INFLORESCENCE erect, 4.5-6.0 (7.5) cm long and 4.0-6.5 cm in diameter, short, cylindric in outline; *primary bracts* 3.7-4.5 cm long, blades 1.6-2.7 cm long and 0.6-1.0 cm wide, green frequently weakly suffused with maroon near margins, spreading, triangular to long triangular, apex narrowly acute to attenuate, sheaths 1.8-2.2 cm long and 2.0-2.5 cm wide, ovate in outline. LATERAL-BRANCHES spreading 1.7-2.4 cm long, collaterally 2-flowered, rarely with a minute vestigial third bud, peduncle 0.2-0.4 cm long, rachis wanting to 0.2 cm long. FLOWERS sessile; *floral bracts* (1.2) 1.6-1.8 cm long and 1.4-1.7 cm wide, green drying to brown, subcoriaceous, lepidote adaxially, subglabrous to immersed lepidote abaxially, ovate to oblong and usually conduplicate along the keel, apex obtuse to rounded or rarely acute; *sepals* 0.7-1.0 cm long and 0.6-0.8 cm wide, green or olive green, drying brown to castaneous, lepidote adaxially, immersed lepi-

dote abaxially, elliptic to broadly ellipitc or rarely suborbicular, apex obtuse to broadly rounded or rarely acute; *petals* 1.7-1.9 cm long and 0.9-1.0 cm wide, white, ovate to obovate constricted medially; *appendages* 0.3 cm long and 1.2 cm wide; *stamens* in a hood configuration over the gynoecium, anthers connivent laterally, filaments 1.2-1.4 cm long, anthers 0.3-0.4 cm long; *ovary* 0.4 cm long and 0.3 cm in diameter, style 1.2 cm long; *capsules* about 1.8 cm long and 0.7 cm in diameter, light castaneous, fusiform.

TYPE: COSTA RICA: SAN JOSÉ PROVINCE: Alto de la Palma de San José on Finca Porvenir in uncut primary forest near streams and in secondary growth and remnant trees in pastures, elev. ca 1500 m, 18 August 1975, *Utley & Utley 2888* (HOLOTYPE: DUKE!, ISOTYPES: CR!, F! and US!).

PHENOLOGY: Flowering specimens have been collected in June.

DISTRIBUTION AND HABITAT: Endemic to Costa Rica between 1400-1900 m in the premontane rain forest life zone and possibly extending slightly into the lower montane rain forest life zone.

DISCUSSION: The most notable features of *V. kathyae* are its relatively short leaves (10.7-22.5 cm) which are green suffused with russet brown abaxially and castaneous sheaths, its floral bracts which exceed the sepals in length, and its extremely short

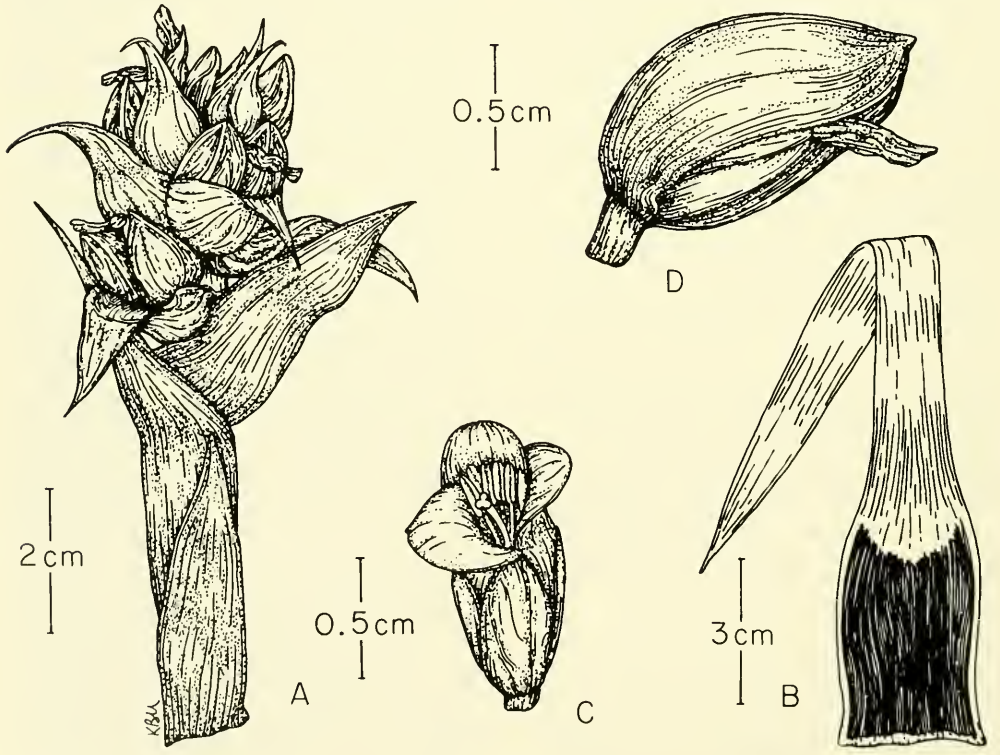


Fig. 24. *Vriesea kathyae*. A. Inflorescence and upper scape; B. Leaf; C. Flower; D. Postanthesis flower with floral bract. From *(Utley & Utley 2568)*.

sepals (0.7-1.0 cm). The inflorescence of *V. kathyae* is erect and short cylindric, bearing white, nocturnal campanulate flowers.

Vriesea kathyae is most similar to *V. hygrometrica* and *V. notata* in habit, its habitat requirements and the general appearance of its inflorescence. The charateristics which distinguish *V. kathyae* from these two taxa are discussed under *V. hygrometrica*. In addition to a general similarity to *V. hygrometrica* and *V. notata, V. kathyae* also has affinities with *V. attenuata*. This is reflected in similarities in leaf size and markings, inflorescence shape and size and primary bract orientation. The differences between these taxa are presented under *V. attenuata*.

ETYMOLOGY: This species is named in honor of Dr. Kathleen Burt-Utley who first brought this taxon to my attention.

SPECIMENS EXAMINED: COSTA RICA: CARTAGO PROVINCE: Tapantí Hydroelectric Project, between 9 and 14 km southeast of Orosí, slopes above the Río Grande de Orosí, 13 December 1974, *Utley & Utley 1620* (DUKE); 20 December 1974, *Utley & Utley 1728* (NOLS); 14 April 1975, *Utley & Utley 3416* (DUKE); 22 March 1976, *Utley & Utley 4350* (DUKE) & *4368* (MO). SAN JOSÉ PROVINCE: between San Jerónimo and Alto de La Palma on Hwy. 3320, 19 June, 1975, *Utley & Utley 2568* (NOLS): region between Cascajal and 8 km northeast on Hwy. 216, 10 December 1975, *Utley & Utley 3616* (DUKE).

26. *Vriesea notata* L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 403. 1953.

Thecophyllum pittieri Mez, Bull. Herb. Boiss. ser. II. 3: 137. 1903, not *Vriesea pittieri* Mez, 1903

TYPE: COSTA RICA: SAN JOSÉ PROVINCE: La Palma, *Tonduz 12526* (HOLOTYPE: B?, n.v. ISOTYPE: US!).

Epiphytic or terrestrial, to 9.0 cm caulescent. LEAVES in a ascending rosette, 21.0-31.0 (39.0) cm long: *blades* 14.0-29.0 cm long and 1.8-4.2 cm wide, green, usually suffused with purple or maroon, with wavy transverse lines or longitudinal stripes, these frequently maroon or brownish maroon, when occuring concomitantly giving a tessellate appearance, maroon suffusion of markings at times alternating with green in a regular pattern resulting in interrupted transverse and longitudinal markings; *sheaths* (7.1) 11.5-13.8 cm long and 3.4-5.4 cm wide, castaneous adaxially, greyish brown abaxially, becoming colored and marked like the blade distally, elliptic to oblong. SCAPE erect to curved erect, 24.0-42.5 (54.0) cm long and 0.3-0.5 cm in diameter; *bracts* 4.6-10.2 cm long, blades 2.0-7.1 cm long and 1.3-2.4 cm wide, green, frequently suffused with maroon or maroon markings, erect to divergent, triangular to ligulate, apex acute to acuminate, sheaths 2.5-3.7 (4.4) cm long and 2.3-4.2 cm wide, ochre, abaxially, frequently with lateral, longitudinal maroon lines ovate or broadly ovate to elliptic. INFLORESCENCE erect, 4.0-9.0 cm long and 5.5-7.0 (10.0) cm in diameter, capitate to subcapitate or short cylindric, frequently elongating in fruit; *primary bracts* 4.5-7.0 cm long, blades 1.9-3.2 cm long and 1.3-2.0 cm wide, pale green, usually with maroon or purple longitudinal lines especially near the margins and frequently with maroon or purple wavy transverse lines, sheaths 2.1-3.5 cm long and 2.3-4.2 cm wide, ovate to elliptic. LATERAL BRANCHES spreading to ascending, (2.5) 3.0-3.8 cm long, collaterally 2-flowered, peduncles 0.0-0.5 cm long, rachis 0.0-0.1 cm long. FLOWERS sessile; *floral bracts* 2.5-3.5 cm long and 1.9-3.2 cm wide, green usually suffused with maroon or red, subcoriaceous, brown-centered lepidote adaxially, immersed lepidote or pitted abaxially, ovate to oblong-ovate or suborbicular, apex broadly acute to obtuse or rounded, occasionally minutely acuminate or apiculate;

sepals 1.2-1.7 cm long and 0.9-1.4 cm wide, green occasionally suffused with red or maroon near the margin, coriaceous, brown-centered lepidote adaxially, immersed lepidote abaxially, elliptic to oblong-elliptic or obovate, apex obtuse to rounded; *petals* about 2.0-3.4 (4.0) cm long and 0.9-1.9 cm wide, white, occasionally weakly suffused with maroon near the margins, ovate to elliptic or oblong-obovate, frequently subfalcate and slightly constricted medially; *appendages* 0.4 cm long and 0.2 cm wide; *stamens* in a hood configuration over the gynoecium, anthers usually connivent by their lateral margins, filaments 1.7-3.0 cm long, anthers 0.3-0.7 (1.0) cm long; *ovary* 0.4-0.5 cm long and 0.3-0.5 cm in diameter, style 1.4-3.1 cm long; *capsules* 1.9-2.7 cm long and 0.7-1.0 cm in diameter, fusiform to subobovate, castaneous.

PHENOLOGY: Flowering specimens have been collected in March through August with an apparent peak in August.

DISTRIBUTION AND HABITAT: Endemic to Costa Rica between 900-2000 m in the premontane and lower montane rain forest life zones, possibly extending into the lower montane wet forest.

DISCUSSION: *Vriesea notata* is characterized by leaves that are usually suffused with red or maroon and have red to maroon wavy transverse lines and longitudinal lines and nocturnal, campanulate corollas. In one population, however, individuals lacked the wavy transverse lines and only possessed colored longitudinal lines. The inflorescence of *V. notata* is short, densely cylindric or subcapitate at anthesis and often elongate post-anthesis. This elongation is so pronounced in some populations that, if the phenomenon were not observed in the field, the elongate and non-elongate forms might well be described as separate taxa.

This variability in inflorescence form in *V. notata* is further aggravated by variation in leaf coloration and markings as well as corolla size. Further studies of variation as well as breeding systems are needed before a realistic evaluation of the relationship of *V. notata* and its closest relative, *V. hygrometrica,* can be made. This problem is discussed further under the latter species.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: 3-5 km west of Cariblanco on the road to Laguna Hule, 16 October 1974, *Utley & Utley 1374* (DUKE); north of San Ramón, between Los Angeles Norte and 7 km north, 15 December 1974, *Utley & Utley 1650* (DUKE), & *1652* (CR); 3-5 km west by west-southwest of Volcán Viejo in the vicinity of Finca Pozo Verde, 24 December 1974, *Utley & Utley 1767* (DUKE, US); between Los Angeles Norte and about 7 km north of La Balsa de San Ramón, 8 August 1975, *Utley & Utley 2776* (DUKE), *2781*(US), & *2785* (CR). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: on hwy. 9 between Cinco Esquinas and the junction of highways 9 and 120, 31 December 1973, *Utley & Utley 583* (DUKE); vicinity of Colonia Virgen del Socorro 3-6 km east of Cariblanco, 10 August 1975, *Utley & Utley 2859* (DUKE). CARTAGO PROVINCE: Tapantí Hydroelectric Project, between 9 and 14 km southeast of Orosí, 5 January 1974, *Utley & Utley 593* (DUKE); 13 December 1974, *Utley & Utley 1593* (DUKE); 20 December 1974, *Utley & Utley 1729* (DUKE, MICH), *1730* (DUKE) & *1731* (F); 14 April 1975, *Utley & Utley 2115* (DUKE); on the road from Tapantí to Tausito/Selva area, 25 August 1975, *Utley & Utley 3009* (DUKE), *3010* (F) & *3011* (NOLS); Tapantí Hydroelectric Project 7-12 km south of the bridge over the Río Grande de Orosí at Tapanti, 5 December 1975, *Utley & Utley 3411* (DUKE), *3419* (CR), *3423* (MO); the northwestern slopes of Volcán Irazu on Hwy. 216 beyond Cascajal, 10 December 1975, *Utley & Utley 3572 A, B, & C* (DUKE, MO, NY), *3600* (GH), *3618* (CAS); Tapantí Hydroelectric Project 7-12 km from the bridge over

the Río Grande de Orosí at Tapantí, 22 March 1976, *Utley & Utley 4349* (NOLS), *4351* (DUKE), *4325* (DUKE); 7 April 1976, *Utley & Utley 4544* (DUKE), & *4545* (F); 25 June 1976, *Utley & Utley 5165* (CR), *5166* (DUKE), *5168*(F) & *5170* (DUKE). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: near the junction of the Interamerican Highway with Hwy. 22 in the Cordillera de Talamanca south of Cartago, 16 April 1975, *Utley & Utley 2180* (DUKE); about 15 km south of Cartago on the Interamerican Highway, 24 August 1975, *Utley & Utley 2949* (DUKE), *2950* (DUKE), *2952* (US), *2953*(CR), & *2954* (NOLS). HEREDIA PROVINCE: region north of Cerro Chompipe or 15 km northeast of Heredia, 15 October 1974, *Utley & Utley 1314* (DUKE); between Vara Blanca and Cinchona on Hwy. 9, 16 October 1974, *Utley & Utley 1332* (DUKE). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: about 5 km northeast of San Isidro de Heredia along the banks of the Río Para Blanco and the lower slopes of Cerro Zurquí, 10 June 1974, *Utley & Utley 957* (DUKE); 18 June 1974, *Utley & Utley 972* (DUKE); 28 May 1976, *Utley & Utley 5102* (DUKE). SAN JOSÉ PROVINCE: between San Jerónimo and Alto de La Palma on Hwy. 330, 15 December 1973, *Utley & Utley 524* (DUKE); 16 December 1973, *Utley & Utley 534* (DUKE); 12 January 1974, *Utley & Utley 607* (DUKE); 4 March 1974, *Utley & Utley 685* (DUKE); 19 June 1975, *Utley & Utley 2565* (DUKE), *2566*(DUKE), *2567* (CAS); 6 July 1975, *Utley & Utley 2588* (US), *2590* (MO), *2592* (DUKE), *2594*(F) & *2595* (DUKE); 18 August 1975, *Utley & Utley 2895* (US), *2896* (CR); between Cascajal and 8 km northeast on Hwy. 216, 23 August 1975, *Utley & Utley 2913* (DUKE), *2939* (GH), *2940* (DUKE), *2941*(MO), *2942* (F) & *2943* (NOLS); between 2 and 5 km southeast of Higuito on Calle Tablazo or 8 to 12 km southeast of Desamparados, 5 September 1975, *Utley & Utley 3034* (DUKE), 4 km north of Cascajal on Hwy. 216, southwestern slopes of Volcán Irazu, 3 July 1976, *Utley & Utley 5273* (DUKE).

27. *Vriesea bracteosa* (Mez & Werckle) L.B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

> *Thecophyllum bracteosum* Mez & Werckle in Mez, Fedde Rep. Spec. Nov. 14: 246. 1916.
> TYPE: COSTA RICA: Province not given, near La Palma, elevation 1500 m *Werckle 17921* (HOLOTYPE: B!, ISOTYPE: GH, photograph US!).

Epiphytic, acaulescent. LEAVES in a subspreading to ascending rosette, 18.0-39.0 (50.5) cm long; *blades* 15.0-19.0 (29.5) cm long and (3.3) 4.2-5.5 cm wide, green, frequently suffused with purple marginally and apically, occasionally with obscure wavy purple lines or mottled areas, ligulate or subligulate to long triangular, apex acute to attenuate or rounded and acuminate, frequently abruptly recurved or spirally involute; *sheaths* 15.5-23.7 cm long and 6.8-9.5 cm wide, pale brown with distal purplish areas or scattered areas of charcoal grey, elliptic to oblong-ovate. SCAPE erect or curved-erect, 36.5-48.0 cm long and 0.7-1.0 cm in diameter; *bracts* 5.9-9.0 cm long, blades 0.8-2.0 cm long and 0.5-1.5 cm wide, green, frequently suffused with purple distally, erect, to recurved or spirally involute, triangular, at times long, narrow triangular, apex acute to attenuate, sheaths 4.4-8.0 cm long and 3.3-3.5 cm wide, green, sheathing erect, ovate to elliptic. INFLORESCENCE erect, 10.5-13.0 cm long and (6.8) 8.0-10.5 cm in diameter, densely cylindric; *primary bracts* 5.1-7.3 cm long, blades 0.9-1.5 cm long and 0.3-1.3 cm wide, green occasionally suffused with maroon distally, ascending, triangular to cuniform in outline, apex acute to narrowly acute or attenuate, sheaths 4.2-6.2 cm long and 3.9-6.0 cm wide, green ovate

to broadly ovate. LATERAL BRANCHES ascending, 3.5-5.0 cm long, collaterally or fasciculately, 2- or 3-flowered, peduncle 0.0-0.2 cm long, rachis 0.0-0.2 cm long. FLOWERS sessile to 0.2 cm pedicellate; *floral bracts* 3.8-4.6 cm long and 3.4-5.4 cm wide, green, subcoriaceous, brown-centered lepidote adaxially and immersed lepidote abaxially, broadly elliptic or ovate to orbicular frequently conduplicately folded along the pronounced keel, apex rounded; *sepals* 2.0-2.5 cm long and 1.5-2.4 cm wide, olive-green, coriaceous, brown centered lepidote adaxially immersed lepidote to glabrous abaxially, elliptic to oblong-elliptic or obovate, apex broadly rounded; *petals* 3.8-4.3 cm long and 1.6-1.8 cm wide, white, obovate; *appendages* 0.5-0.7 cm long and 0.2-0.3 cm wide; *stamens* in a hood configuration over the gynoecium, usually weakly connivent by the lateral margins of the anthers, filaments 3.0-3.5 cm long, anthers 0.9-1.0 cm long; *ovary* about 0.6 cm long and 0.5-0.6 cm in diameter, style 2.6-2.9 cm long; *capsules* 4.1-5.3 cm long and 1.3-1.6 cm in diameter, castaneous, fusiform.

PHENOLOGY: Flowering specimens have been collected in June, July and October.

DISTRIBUTION AND HABITAT: Endemic to Costa Rica between 1500-1900 m in the lower montane and premontane rain forest life zones.

DISCUSSION: The inflorescence of *Vriesea bracteosa* is short, dense cylindric or subcapitate with large, coriaceous primary bracts which are more or less imbricate at anthesis. The unmarked leaves typically form an ascending rosette. Like *V. capitata*, the inflorescence of *V. bracteosa* is usually covered with a gelatinous matrix. The white, campanulate, nocturnal flowers of this taxon are exserted beyond the primary bracts. *Vriesea bracteosa* was originally described by Mez and Werckle (in Mez, 1916) as having three flowers in the axils of the lower primary bracts. However, specimens have also been collected which have two flowers in the axils of the lower primary bracts.

Vriesea bracteosa is undoubtedly most closely related to *V. capitata*, which it superficially resembles. These taxa share a series of common characters, including rosette form, leaf shape, inflorescence form, floral morphology and gelatinous matrix. Beyond these characters, *V. bracteosa* and *V. capitata* have a distinctive leaf anatomy which has not been observed in other thecophylloid vrieseas. In both species, the adaxial hypodermis is interrupted by a well developed layer of extrafascicular sclerenchyma. Although both taxa occur in the pass area between Volcan Barba and Volcan Irazu in the Cordillera Central, they have not been encountered growing sympatrically. Within this area *V. bracteosa* is typically found at slightly higher elevations (1500-1900 m) than *V. capitata* (900-1400 m).

Although *V. bracteosa* and *V. capitata* may be difficult to distinguish on the basis of vegetative morphology alone, they are easily distinguished from each other in flower or fruit. In addition to subtle differences in the nature of their inflorescences, *V. bracteosa* and *V. capitata* are separated by floral bract shape and length and petal length. Moreover, the adaxial leaf surfaces of *V. capitata* are densely, cinereously pubescent, whereas those of *V. bracteosa* are not. Although this may be an artifact of leaf weathering which resulted in trichome loss, this character is constant in all my collections of *V. bracteosa*.

SPECIMENS EXAMINED: COSTA RICA: CARTAGO PROVINCE: 5-6 km south of San Isidro de Cartago on the Interamerican Highway, 28 February 1975, *Utley & Utley 1907* (DUKE); on the road from Tapanti to Taus and Tausito, between 1 and 4 km beyond the bridge over the Río Grande de Orosi, 31 July 1976, *Utley & Utley 5588* (MO), *5608* (DUKE) & *5609* (US). BORDER OF CARTAGO AND SAN JOSÉ PROVINCES: along the Interamerican

Highway about 20 km south of Cartago, in the vicinity of Casa Mata, 17 March 1975, *Utley & Utley 1996* (DUKE), *1997* (CR), *1998* (F). BORDER OF HEREDIA AND SAN JOSÉ PROVINCES: along the Rio Para Blanco in the vicinity of Cerro Zurquí, 30 March, 1974, *Utley & Utley 723* (DUKE); 15 October 1974, *Utley & Utley 1284* (NOLS). SAN JOSÉ PROVINCE: between San Jerónimo and Alto de La Palma on Hwy. 220, 29 June 1974, *Utley & Utley 979* (DUKE); 19 June 1975, *Utley & Utley 2562* (DUKE); between Cascajal and 8 km northeast on Hwy. 216, 23 August 1975, *Utley & Utley 2924* (NOLS); 7-10 km southeast of Desamparados in the Altos de Tablazo, 2 July 1976, *Utley & Utley 5233* (DUKE); at Cascajal about 3 km north of Las Nubes on Hwy. 216, the northwest slopes of Volcán Irazu, 3 July 1976, *Utley & Utley 5248* (NY) & *5272* (DUKE).

28. *Vriesea capitata* (Mez & Werckle) L. B. Smith & Pitt. J. Wash. Acad. Sci. 43: 402. 1953.

> *Thecophyllum capitatum* Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 873. 1904.
> TYPE: COSTA RICA: no location given, *Werckle Bromel. Costaric. 86* (HOLOTYPE: B!, photograph US!).

Epiphytic, acaulescent to 5.5 cm caulescent. LEAVES in an ascending to suberect rosette, 23.7-40.0 cm long; *blades* 11.5-17.5 cm long and 3.6-4.5 cm wide, green frequently suffused with purple or maroon distally, ligulate apex acute to rounded and apiculate; *sheaths* 12.0-17.0 cm long and 5.5-7.0 cm wide, castaneous abaxially, brown adaxially, margins suffused with purple to maroon distally. SCAPE erect, 22.5-35.0 cm long and 0.4-1.0 cm in diameter; *bracts* 4.2-7.6 cm long, blades 1.2-2.6 cm long and 1.1-2.0 cm wide, green drying to brown, erect or frequently recurved, triangular or short ligulate, apex attenuate to acute or rounded and abruptly acuminate, sheaths 2.6-5.0 cm long and 2.1-3.3 cm wide, drying ochre or brown castaneous proximally, sheathing erect, ovate to elliptic or oblong elliptic. INFLORESCENCE erect, 3.5-6.5 cm long and 4.0-6.5 cm in diameter, subcapitate; *primary bracts* 2.3-3.8 cm long, blade 0.7-1.4 cm long and 0.5-1.4. cm wide, green becoming brown at anthesis, spreading, triangular, apex acute, sheaths 1.9-2.9 cm long and 2.2-2.6 cm wide, green elliptic to ovate in outline. LATERAL BRANCHES ascending, 3.8-5.2 cm long, subcollaterally 2-flowered, peduncle 0.1-0.3 cm long rachis about 0.4 cm long. FLOWERS sessile, *floral bracts* 2.0-2.2 cm long and 1.3-1.6 cm wide, green subcoriaceous, brown-centered lepidote adaxially, glabrous abaxially, oblong to obovate, unkeeled or very weakly keeled distally, apex obtuse; *sepals* 2.0-2.2 cm long and 1.3-1.6 cm wide, olive green, coriaceous, brown-centered lepidote adaxially, glabrous abaxially, elliptic to obovate, apex obtuse; *petals* about 3.1-3.4 cm long and 1.5-1.6 cm wide, white, obovate; *appendages* 0.4 cm long and 0.2-0.25 cm wide; *stamens* in a hood configuration over the gynoecium, filaments about 2.3 cm long anthers about 0.7 cm long; *ovary* about 0.7 cm long and 0.5 cm in diameter, style 1.7 cm long; *capsules* 4.1 cm long and 0.8-1.0 cm in diameter, casteneous, fusiform.

PHENOLOGY: Flowering plants have been collected only during August.

DISTRIBUTION AND HABITAT: Known from Costa Rica and a few recent collections from Cerro Jefe in Panamá. Collected between 900-1400 m in premontane rain forest life zone possibly extending slightly into the premontane wet forest life zone.

DISCUSSION: *Vriesea capitata* remains a poorly collected taxon. In locations where I have collected this species, I have never seen more than one or two individuals in flower or fruit. It is characterized by its rigidly coriaceous leaves in a subascending to suberect

rosette, subcoriaceous primary bracts which are divergent to subspreading at anthesis, and its subcapitate inflorescence. The inflorescence of *V. capitata* is often totally covered with a gelatinous exudate. The developing floral buds are immersed in this gelatinous matrix until anthesis, at which time the white, campanulate nocturnal flowers emerge. When the atmospheric humidity is low, this exudate will dry on the flower buds and inhibit anthesis.

Vriesea capitata is most closely related to *V. bracteosa* and the characters which distinguish these taxa are discussed under the latter species.

SPECIMENS EXAMINED: COSTA RICA: ALAJUELA PROVINCE: along road between Hwy. 9 and Laguna Hule between 0.5-5.0 km northwest of Cariblanco, 16 October 1974, *Utley & Utley 1368* (DUKE); north of San Ramon, between Los Angeles Norte and about 7 km north, 15 December 1974, *Utley & Utley 1635* (CR) & *1651* (DUKE). BORDER OF ALAJUELA AND HEREDIA PROVINCES: vicinity of Colonia Virgen del Socorro about 3-6 km east of Cariblanco, 10 August 1975, *Utley & Utley 2878* (DUKE). BORDER OF HEREDIA AND SAN JOSE PROVINCES: about 5 km northeast of San Isidro de Heredia on Calle Yerbabuena, 3 April 1976, *Utley & Utley 4475* (NOLS) & *4477* (DUKE). PANAMA: PANAMA PROVINCE: Cerro Jefe, December 1974, *Mori & Kallunki 3619* (MO), 18 December 1974, *Mori & Kallunki 3800* (MO).

DOUBTFUL AND EXCLUDED SPECIES

Vriesea discolor (Mez & Werckle) L.B. Smith & Pitt. J. Wash. Acad. 43: 402. 1953.

> *Thecophyllum discolor* Mez & Werckle in Mez, Fedde, Rep. Spec. Nov. 14: 246. 1916.
>
> TYPE: COSTA RICA: without further location, "Werckle."

Mez (1916) did not cite a specific collection when he described *Thecophyllum discolor*. Moreover, no specimen of this taxon is on deposit at the Berlin-Dahlem Herbarium, which acquired Mez's personal collection of Bromeliaceae in 1936.

The original diagnosis of *Thecophyllum discolor* agrees with the description and type collection of the earlier *Thecophyllum latissima*, but the taxa reportedly differ in the number of flowers per lateral inflorescence branch (four or five in *Th. latissimum* versus up to 12 in *Th. discolor*). The only putative material of *V. discolor* I have seen is *Werckle 12* (US) which has 4 to 6 flowers per lateral inflorescence branch and is undoubtedly *V. latissima*. In all likelihood *V. discolor* is a synonym of *V. latissima* but until authentic material is available the former should be maintained as a doubtful species.

Vriesea spectabilis (Mez & Werckle) L.B. Smith & Pitt. J. Wash. Acad. 43: 403. 1953.

> *Thecophyllum spectabile* Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 873. 1904.
>
> TYPE: COSTA RICA: without further locality, *Werckle s.n.* (HOLOTYPE: B!, photograph US!).

Recent flowering collections have shown that this taxon has connate sepals and petals and the species has been transferred to *Guzmania* (Utley, 1978).

Vriesea splitgerberi (Mez) L.B. Smith & Pitt. J. Wash. Acad. 43: 403. 1953.

> *Guzmania splitgerberi* Mez in DC. Monogr. Phan. 9: 930. 1896.
>
> TYPE: SURINAME: Blauwe Berg, upper Suriname River, *Splitgerber 966* (HOLOTYPE: L!, photograph US!).
>
> *Thecophyllum splitgerberi* (Mez) Pitt. Evolution 2: 60. 1948.

This species displays the thecophylloid syndrome of reduced lateral branches and enlarged primary bracts. However, *V. splitgerberi* differs from all other thecophylloid vrieseas in its polystichous lateral inflorescence branches. Moreover, the stigmatic surface consists of three, solid, cylindrical branches (Fig. 15a) rather than the 3-cupped stigmatic structure typical of the thecophylloid vrieseas and their allies. In light of this I feel that this species is not closely allied to the thecophylloid vrieseas and I have excluded it from this treatment.

Vriesea vittata (Mez & Werckle) L.B. Smith & Pitt. J. Wash. Acad. 43: 403. 1953.

> *Thecophyllum vittatum* Mez & Werckle in Mez, Bull. Herb. Boiss. ser. II. 4: 871. 1904.
> TYPE: COSTA RICA: without exact locality, *Werckle Brom. Costar. 79* (HOLOTYPE: B!, photograph US!).

A through examination of the type material of this species failed to reveal any evidence of two bracts subtending the single flowers. Moreover, numerous collections which are essentially identical to the type of *V. vittata* also have simple inflorescences with flowers subtended by single bracts rather than two bracts as stated by Mez. The affinities of this species seem to be with the thecophylloid allies (cf.p. 18) and not the taxa with compound inflorescences considered in this treatment.

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RESUMEN

Los thecophylloid vrieseas habian sido mantenidos por mucho tiempo en un género distinto, *Thecophyllum*, por razón de sus brácteas agrandadas y ramas florescentes secundarias reducidas. Ahora, estas especies forman una taxa de alianza cohesiva geográficamente y morfólogicamente dentro de las sección *Xiphion* de *Vriesea*. Aparte de las flores nocturnales que generalmente se encuentran en la sección *Xiphion*, varios thecophylloid vrieseas demuestran un periodo crepuscular y diurno y sindromes florales que sugieren una gran adaptación de vectores de polen. Claves, descripción y sinonomías se dán para la taxa que pertenece a México y América Central y su afinidad es discutida. *Vriesea greenbergii*, *V. kathyae*, *V. luis-gomezii* y *V. lyman-smithii* han sido ilustradas y descritas como especies nuevas.

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TULANE STUDIES IN ZOOLOGY AND BOTANY

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FISHES OF THE BAYOU SARA DRAINAGE, LOUISIANA AND MISSISSIPPI, WITH A DISCRIMINANT FUNCTIONS ANALYSIS OF FACTORS INFLUENCING SPECIES DISTRIBUTION

JAMES M. GRADY[1], ROBERT C. CASHNER AND JAMES S. ROGERS

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ABSTRACT

A fish survey of Bayou Sara, a southward flowing tributary to the lower Mississippi River in Mississippi and Louisiana, was conducted between June 1976 and May 1979. Eighty species, representing 17 families are known from the system as a result of survey work in the lower reaches by Louisiana State University, Baton Rouge, and our work in the upper and middle sections of Bayou Sara. Bayou Sara has fewer species than the adjacent Thompson Creek and nearby westward flowing Buffalo Bayou. The species composition is notable in comparison to the other two systems by the absence of common species of petromyzontids, ictalurids and cyprinodontids. Of the families shared by the three drainages, Bayou Sara most closely resembles Thompson Creek.

Distributional data from six permanent collection stations were supplemented with measurements for 17 environmental parameters. The combined data were subjected to a multiple discriminant functions analysis to identify significant environmental variables accounting for the separation of fish distributions. A single discriminant function, principally contributed to by stream position, accounted for 79% of the variance among fish distributions.

INTRODUCTION

The eastern embayment of the lower Mississippi River receives several small to moderate-sized tributaries in southwestern Mississippi and southeastern Louisiana. The major westward flowing tributaries are Big Black River, Bayou Pierre, Coles Creek, and Homochitto and Buffalo rivers. The lowermost tributaries are Tunica Bayou, Bayou Sara and Thompson Creek (Fig. 1).

This region of the lower Mississippi River drainage, the tributaries to the Lake Pontchartrain estuary, and the Pearl River drainage have been extensively surveyed by R.D. Suttkus (Tulane University), N.H. Douglas (Northeast Louisiana University), J.V. Conner (Louisiana State University), and their students, on either a regular or sporadic basis for the past 30 years. In addition, intensive fish faunal surveys have been conducted in Thompson Creek (Guillory, 1981, 1982), Buffalo Bayou (Cashner et al., 1976), Tchefuncte River (Saul, 1974) and Amite

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River (Laiche, 1980). Douglas (1974) provided comprehensive distributional data for many species in the state.

Zoogeographically the lower Mississippi embayment eastward to the Pearl River yields a number of distinctive distributional patterns for its indigenous species, as first noted by Guillory and Conner (1973), and discussed in detail by Guillory (1982).

Bayou Sara is one of the southernmost tributaries to the eastern embayment of the Mississippi River (Fig. 1) and is centrally located in this area of engimatic distributions. In an effort to clarify some species distributions, a study of the ichthyofauna of the Bayou Sara system was initiated in June 1977 and included monthly sampling from the headwaters to the mouth until March 1979. Although numerous collections had been made in the system by R.D. Suttkus and J.H. Caruso, a comprehensive survey of the Bayou Sara fishes has not been previously reported.

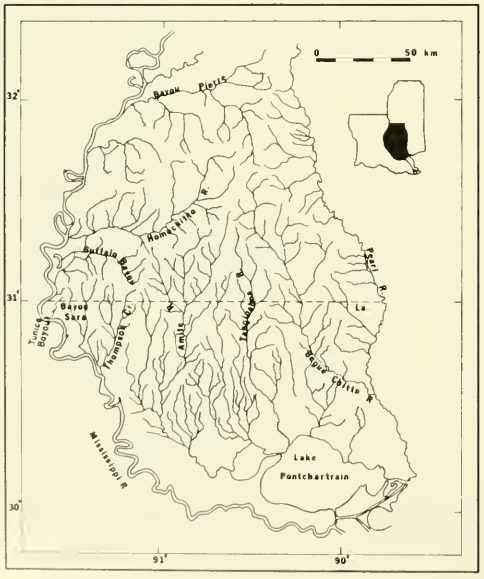

Figure 1. Bayou Sara study area and adjacent drainages.

A second aspect of this study centered on a physico-chemical characterization of Bayou Sara and an attempt to determine associations between environmental parameters and observed patterns of fish distribution. A number of statistical procedures have been utilized in attempts to produce reliable quantitative associations between physical and chemical factors and the distribution of fishes (Smith and Fisher, 1970; Smith and Powell, 1971; Moyle and Nichols, 1973; Wallace, 1973; Stevenson et al., 1974; Heins and Clemmer, 1975; Rogers et al., 1976; Sobczak, 1976; Baker and Ross, 1981). Discriminant functions analysis was selected to identify significant environmental parameters influencing instream fish distributions in Bayou Sara.

Description Of Study Area

Bayou Sara originates in Wilkinson Co., Mississippi, west of Woodville. The stream flows in a southward direction for 56.6 km before entering the Mississippi River near St. Francisville, Louisiana, at river mile 266. It drains approximately 493 km^2, including portions of Wilkinson Co., Mississippi and West Feliciana Parish, Louisiana.

Bayou Sara traverses several geologic formations along its course. In headwater regions, the stream cuts through and exposes the Citronelle formation, a Pliocene-Pleistocene alluvial formation characterized by coarse sand, silt, and gravel (Fisk et al., 1938; Fisk, 1944; Murray, 1961; Sibley, 1972). Partial erosion of the Citronelle has exposed brightly colored clays and coarse gravels of older Tertiary formations at some headwater locations.

Sand substrates predominate in the headwater section of Bayou Sara, but gravel and hard packed clay are conspicuous in riffle areas. Turbidity is the lowest in the headwaters, although organic debris is abundant during several

months of the year. Terrestrial vegetation providing stream cover and allocthonous detritus is heaviest in this region of Bayou Sara. A mixed hardwood and coniferous forest with sweetgum (*Liquidambar styraciflua*), basswood (*Tilia sp.*), water oak (*Quercus nigra*), short leaf pine (*Pinus echinata*), and loblolly pine (*P. taeda*) is the dominant community type (Caplenor et al., 1968). Deep cut banks are prevalent in headwater areas where Bayou Sara occupies a narrow channel (0.5-1.0 m) with alternating pools and riffles.

Further downstream, Bayou Sara encounters four or five broad step-like depositional surfaces, the Pleistocene Terraces (Fisk et al., 1938; Fisk, 1944; Murray, 1961). Soft, shifting sand substrates with patches of fine gravel are characteristic of the terrace areas. Current velocity decreases and tubidity increases in this region of alternating sand bottomed runs and pools.

A small portion of lower Bayou Sara cuts through the Recent Mississippi River flood plain (Fisk et al., 1938). This Recent flood plain is separated from the Pleistocene Terraces by the eastern escarpment of the Mississippi River. Here water levels and other environmental conditions reflect the influence of the Mississippi River. The lower reaches are characterized by large accumulations of silt, slight current, and highly turbid waters. Bayou Sara occupies a broad, shallow basin with depths ranging from 15 cm to 1.5 m and widths ranging from 25 to 60 m during periods of low flow in the Mississippi River.

In the extreme headwaters many small tributaries are occasionally intermittent during summer and early fall. The main channel, however, is spring-fed and has permanent flow year round. Water levels along the watercourse fluctuate with the seasonality of rainfall and prevailing conditions in the Mississippi River. Stream flow is heaviest during winter and spring, which are the usual periods of heavy rainfall (Snows, 1970).

Materials And Methods

A. Physico-chemical Analysis

Water quality determinations, physical measurements and fish collections were taken at selected stations along the main channel of Bayou Sara from February, 1978 through March, 1979. Five stations (Stations 1-5 in Fig. 2) were initially selected for monthly physico-chemical measurements. However, time limitations, due to concurrent fish sampling, dictated an alternative sampling procedure. Three stations were visited one month and the remaining two the next. This system was followed for three months, but then modified so that 17 environmental parameters and fish collections were taken at all five stations bimonthly. Due to high water and flooding, Station 2 became inaccessible after April,

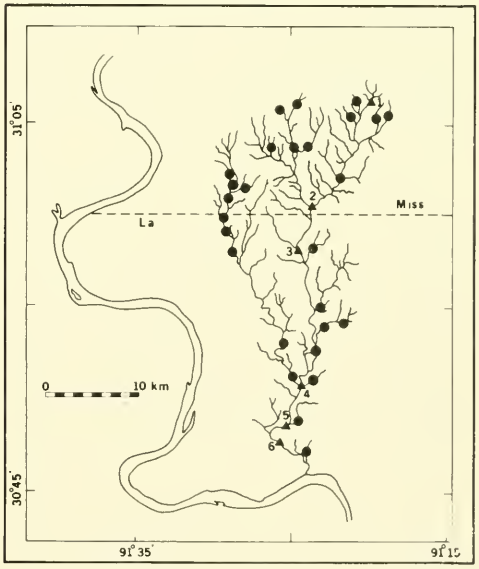

Figure 2. Bayou Sara study area, indicating locations of the 6 permanent stations (triangles) and the 27 supplemental sampling stations (circles).

1978. The close proximity of Station 3 lessened the loss of this sampling site. A downstream site, Station 6,was added in December, 1978.

Conductivity, dissolved oxygen, and water temperature were measured in the field with a YSI Model 33 S-C-T Meter and a YSI Model 51B Oxygen Meter. Additional field measurements included the titrimetric determination of free carbon dioxide and alkalinity, and the colorometric measurement of pH utilizing a Rascher and Betzold Colorometric kit. The remaining chemical analyses, turbity, suspended solids, and total solids, were conducted in the laboratory. Turbidity measurements were made with a Hellige Turbidimeter and evaporation and ashing techniques were used for total and suspended solids determinations.

U.S. Geological Survey topographic maps (1:24,000) were used to determine stream position, stream order, gradient and altitude. Stream order was calculated according to Horton's (1945) method as modified by Strahler (1957). Measurements of mean depth, mean width and current velocity were made according to Lagler (1956). Cross-sectional area was computed following Sobczak (1976).

B. Fish Collections

A survey of the Bayou Sara system was begun in June, 1977 and continued until December, 1977. Fish collections were made concurrently with physico-chemical measurements at five or six of the permanent stations from February, 1978 to March, 1979. Supplemental collections, in addition to those made in 1977, were made at localities throughout the Bayou Sara system to establish as complete a faunal list as possible. Collection sites are shown in Fig. 3. Fishes were collected with 3.3 m, 4.8 mm nylon mesh seines and originally preserved in 10% formalin.

C. Data Analysis

A multiple discriminant functions analysis subroutine of Nie et al. (1975) was employed to identify environmental parameters contributing to the spatial separation of species. The value of this technique was discussed by Green (1971). Both direct and stepwise methods of discriminant analysis were utilized in this study. The direct method enters all of the independent variables into the analysis concurrently. The discriminant functions are then fitted directly from the entire set of variables. Stepwise discriminant functions analysis permits the exclusion of variables containing little information. Environmental variables are selected for inclusion into the analysis on the basis of their discriminating power. The criterion for establishing discriminating power in this analysis was Rao's V, a generalized distance measure. Those variables which contributed to the largest increase in V, when added to the previous variables, were selected.

Forty-three groups representing the 43 species collected at the permanent stations were designated for input into the analysis. Mean discriminant scores were generated for each of these groups based on the seventeen parameters (13 field and lab measurements plus 4 stream features calculated from topographic maps) measured at the time each species was

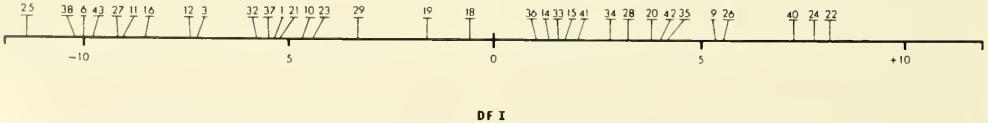

Figure 3. Mean discriminant scores for the first discriminant function (DF I) of the stepwise analysis.

captured.

Several modifications were introduced following the initial analysis. A minimum inclusion level for each group was established following Green (1971). Only those species present in at least two collections at permanent stations were included in subsequent analyses, thereby reducing the number of groups to 33. Because a uniform sampling technique was not employed at each site for the collection of fish, data sets were not weighted by species abundance.

Results

A. Physico-chemical Analysis

Means, ranges and standard deviations of thirteen of the physical and chemical measurements from each of the six stations are presented in Table 1. Because stream position, gradient, altitude and stream order are relatively static, only the observed values are presented in Table 2.

B. Distribution of Fishes

A total of 42,867 specimens was taken in 65 collections at 33 localities in the Bayou Sara system (Fig. 2). Forty-three species, representing 13 families and 27 genera, were collected during the two year study and records for nine more species were obtained from Douglas (1974) and from collection records at the Tulane Museum of Natural History. John Van Conner kindly provided records of an additional 28 species taken primarily in the lower part of the system during surveys by personnel in the Department of Fisheries, Louisiana State University, Baton Rouge. These records include four species represented only by larvae and at least eight species that could potentially range into the main portion of our study area. A complete list of all 80 species from 17 families documented from the Bayou Sara system is presented in Table 3. Nomenclature given follows Robins et al. (1980).

C. Data Analysis

A maximum of 17 discriminant functions (DF) was extracted during the direct analysis, five of which accounted for 70% of the among-species variance (Table 4). Standardized DF coefficients for the 17 environmental variables for these five DF are also presented in Table 4. The magnitude of the coefficients indicates the relative contribution of each variable to the formation of the DF. Thus altitude and stream position provided the major contributions toward the separation of groups in DF I, which accounted for slightly over 30% of the among-species variance. These two physical parameters remained the most significant factors contributing to the overall separation of the groups (species) in the remaining 16 DF. Total solids and stream order were the only other variables contributing to group separation in all of the 17 DF. Comparisons of the magnitude of the DF coefficients for these parameters, with those for altitude and stream position, reveal, however, that their contributions are only minor. None of the DF extracted during the direct analysis reached a high degree of statistical significance ($p > .05$).

The distributional data and associated environmental parameters were also subjected to a stepwise DF analysis. Two variables, water temperature and stream position, were selected for inclusion into the analysis based on their discriminating power as indicated by a significant increase in Rao's V (Table 5). Discriminant function 1 accounted for almost 79% of the among-species variance and was significant ($p < .01$). The analysis weighted most heavily on stream position. Although DF II accounted for over 21% of the among-species variance, it failed to attain as high a degree of significance ($p > .05$).

TABLE 1. Means, Ranges, and Standard Deviations of 13 Physico-Chemical Parameters at the 6 Permanent Stations in Bayou Sara

Station	Total Alkalinity (mg/l)	Free CO_2 (mg/l)[c]	pH	Conductivity (mhos/cm^2)	Total Solids (mg/l)	Suspended Solids (mg/l)	Turbidity (mg/l)
1	35[a]	9.00	7.01	75	91.04	24.45	2.63
	20[b]	7.14	0.16	61	87.80	25.39	4.77
	14-72[c]	1.60-22.0	6.80-7.30	20-215	28.15-293.46	1.31-60.11	0.00-14.00
2	37	1.40	7.13	53	48.65	14.35	0.33
	29	0.17	0.06	5	28.29	1.80	0.29
	20-71	1.20-1.50	7.10-7.20	50-59	32.30-81.32	13.31-16.43	0.00-0.50
3	53	1.19	8.03	82	74.41	29.17	2.84
	21	1.58	0.55	26	36.52	40.57	4.38
	22-78	0.00-3.50	7.00-8.60	40-117	42.23-148.52	3.31-103.31	0.00-11.70
4	46	5.70	7.33	95	180.29	90.30	17.91
	16	5.05	0.16	40	180.40	123.10	17.91
	28-68	0.00-10.90	7.00-7.50	40-180	60.00-582.10	7.50-362.45	0.30-55.30
5	43	8.93	7.28	98	84.27	18.09	5.55
	11	7.86	0.15	27	11.76	24.58	5.87
	33-60	2.40-23.90	7.10-7.50	71-143	66.66-94.72	3.37-67.42	0.00-12.40
6	59	11.25	7.50	91	92.84	28.34	0.20
	13	1.77	0.14	1	17.81	26.64	0.28
	50-68	10.00-12.50	7.40-7.60	90-92	80.25-105.43	9.50-47.18	0.00-0.40

a-mean; b-standard deviation; c-range

Discussion

A. Physico-chemical Factors

Progressional changes in the 17 environmental parameters are evident in Table 1. Values for pH, alkalinity, conductivity, total and suspended solids, turbidity, temperature, mean depth, mean width and cross-sectional area increase downstream. These successively higher values can be attributed to the expected reduction of current velocity and greater accumulations of allocthonous material. Additionally, the progressive downstream rise in temperature is also influenced by the predominance of sand substrates and a reduction of cover associated with reduced riparian vegetation.

Spatial differences in some of the variables can be attributed to the influence of localized conditions. High levels of free CO_2 and correspondingly lower pH values at Station 1 are due in part to increased deposition of organic material deposited in this area. Turbidity, conductivity, and dissolved and suspended solids at Station 1 were relatively high for an upstream location. Heavy detrital input partially accounts for these high values, but a fallen tree dam acted to further increase the readings. The obstruction also caused higher values for mean depth and width, and cross-sectional area, while decreasing flow rates.

Localized conditions also caused high readings for turbidity, suspended and total solids, and conductivity at Station 4, where a gravel washing operation dramatically increased the suspended particulate matter. At Station 3 the possible presence of lime deposits upstream could explain the consistently high pH and low CO_2 values.

Overall, the deviations from the observed progressional trends from stations 2-6 are probably the result of reduced sampling effort. Still, despite the influence of

TABLE 1 CONT.

Dissolved Oxygen (mg/l)	Temperature (°C)	Current (m/sec)	Mean Depth (m)	Mean Width (m)	Cross-sectional Area (m^2)
9.73	18.86	0.38	0.13	5.49	0.72
2.62	7.26	0.27	0.07	1.13	0.41
7.20-14.40	10.20-28.00	0.12-0.77	0.07-0.27	3.53-6.82	0.3-1.59
13.23	14.27	0.21	0.10	11.80	1.19
0.95	7.39	0.09	0.01	2.69	0.35
12.50-14.30	10.00-22.80	0.16-0.31	0.10-0.11	10.25-14.90	0.99-1.60
9.89	20.63	0.60	0.15	22.98	3.56
1.76	8.75	0.34	0.04	7.39	1.46
7.70-12.10	10.30-29.50	0.18-1.23	0.11-0.20	7.73-31.25	0.91-5.10
8.51	26.76	0.24	0.34	23.98	8.26
2.18	11.58	0.16	0.11	10.15	5.74
6.50-11.50	10.10-37.80	0.14-0.55	0.18-0.45	17.63-46.15	4.05-20.94
8.75	27.15	0.27	0.24	32.00	7.34
1.48	7.75	0.10	0.09	7.10	2.54
7.70-10.80	14.40-34.00	0.16-0.42	0.12-0.32	23.50-40.50	3.97-10.31
9.45	19.75	0.44	0.12	32.82	3.98
1.77	6.72	0.06	0.03	0.78	1.20
8.20-10.70	15.00-24.50	0.39-0.48	0.10-0.14	32.27-33.37	3.13-4.82

localized conditions and sampling error, measurements for the 17 variables fall within the ranges for those reported from comparable stations in adjacent Buffalo Bayou (Rogers et al., 1976) and Thompson Creek (Guillory, 1974).

B. Fish Distributions

Intersystem Distribution. Bayou Sara, like Thompson Creek, has a more depauperate fauna than the larger, westward flowing tributaries to the eastern Mississippi Embayment and adjacent Lake Pontchartrain

TABLE 2. Stream Position, Gradient, Altitude, and Stream Order at Six Physico-Chemical Stations.

Station	Stream Position (km)	Gradient (m/km)	Altitude (m)	Stream Order
1	59.29	5.33	79.26	3.00
2	42.00	1.54	54.86	4.00
3	36.35	1.54	42.67	5.00
4	16.29	0.76	18.29	5.00
5	10.50	0.76	12.19	5.00
6	7.93	1.14	9.14	5.00

TABLE 3. List of Species known to occur in Bayou Sara Drainage, Mississippi and Louisiana. (X= collected during present study; D= record from Douglas, 1974; TU= Tulane University Museum of Natural History Record; L= LSU record; *= likely to occur in study area).

SPECIES	SOURCE
LEPISOSTEIDAE	
Lepisosteus oculatus - spotted gar	X
Lepisosteus osseus* - longnose gar	L
Lepisosteus platostomus - shortnose gar	X
AMIIDAE	
Amia calva - bowfin	L
ANGUILLIDAE	
Anguilla rostrata* - American eel	TU
CLUPEIDAE	
Alosa chrysochloris* - skipjack herring	L
Dorosoma cepedianum - gizzard shad	X
Dorosoma petenense - threadfin shad	X
HIODONTIDAE	
Hiodon alosoides - goldeye	L
ESOCIDAE	
Esox americanus - grass pickerel	L
CYPRINIDAE	
Cyprinus carpio - common carp	X
Hybognathus hayi cypress minnow	D
Hybognathus nuchalis - Mississippi silvery minnow	X
Hybopsis aestivalis - speckled chub	X
Nocomis leptocephalus - bluehead chub	X
Notemigonus crysoleucas - golden shiner	X
Notropis atherinoides - emerald shiner	X
Notropis blennius - river shiner	X
Notropis buchanani - ghost shiner	L
Notropis camurus - bluntface shiner	X
Notropis chrysocephalus - striped shiner	X
Notropis emilae - pugnose minnow	TU
Notropis fumeus - ribbon shiner	TU
Notropis longirostris - longnose shiner	X
Notropis lutrensis - red shiner	X
Notropis shumardi* - silverband shiner	L
Notropis texanus - weed shiner	TU
Notropis umbratilis - redfin shiner	X
Notropis venustus - blacktail shiner	X
Notropis volucellus - mimic shiner	X
Pimephales notatus - bluntnose minnow	X
Pimephales vigilax - bullhead minnow	X
Semotilus atromaculatus - creek chub	X
CATOSTOMIDAE	
Carpiodes carpio - river carpsucker	X
Cycleptus elongatus - blue sucker (larvae only)	L
Erimyzon oblongus - creek chubsucker	X
Erimyzon sucetta - lake chubsucker (larvae only)	L
Hypentelium nigricans* - northern hogsucker	L
Ictiobus bubalus - smallmouth buffalo	X
Ictiobus cyprinellus - bigmouth buffalo	L
Minytrema melanops - spotted sucker (larvae only)	L

TABLE 3. CONT.

SPECIES	SOURCE
ICTALURIDAE	
Ictalurus furcatus - blue catfish	L
Ictalurus melas - black bullhead	L
Ictalurus natalis - yellow bullhead	X
Ictalurus puntatus - channel catfish	X
Pylodictus olivaris - flathead catfish	L
APHREDODERIDAE	
Aphredoderus sayanus* - pirate perch	L
CYPRINODONTIDAE	
Fundulus olivaceus - blackspotted topminnow	X
POECILIIDAE	
Gambusia affinis - mosquitofish	X
Poecilia latipinna - sailfin molly	L
ATHERINIDAE	
Labidesthes sicculus - brook silverside	X
Menidia beryllina* - inland silverside	L
PERCICHTHYIDAE	
Morone chrysops - white bass	X
Morone mississippiensis - yellow bass	L
CENTRARCHIDAE	
Centrarchus macropterus - flier	L
Elassoma zonatum - banded pygmy sunfish	X
Lepomis cyanellus - green sunfish	X
Lepomis gulosus - warmouth	TU
Lepomis humilis - orangespotted sunfish	TU
Lepomis macrochirus - bluegill	X
Lepomis marginatus - dollar sunfish	L
Lepomis megalotis - longear sunfish	X
Lepomis microlophus - redear sunfish	L
Lepomis punctatus - spotted sunfish	L
Lepomis symmetricus - bantam sunfish	L
Micropterus punctulatus - spotted bass	X
Micropterus salmoides - largemouth bass	X
Pomoxis annularis - white crappie	X
Pomoxis nigromaculatus - black crappie	X
PERCIDAE	
Etheostoma asprigene - mud dater	L
Etheostoma caeruleum - rainbow darter	X
Etheostoma chlorosomum* - bluntnose darter	L
Etheostoma gracile - slough darter	D
Etheostoma parvipinne - goldstripe darter	D
Etheostoma proeliare* - cypress darter	L
Etheostoma whipplei - redfin darter	X
Percina ouachitae - saddleback darter	X
Stizostedion canadense - sauger (larvae only)	L
SCIAENIDAE	
Aplodinotus grunniens - freshwater drum	X

drainages (Guillory, 1981). Unfortunately, there is little published on the ichthyofauna of the streams in this region, except for Douglas (1974), Guillory (1981, 1982) and several Master's and Doctoral theses (Saul, 1974; Sobczak, 1976; Laiche, 1980). The number of species known from the two southward flowing lower Mississippi River tributaries, Thompson Creek and Bayou Sara, is similar with 89 and 80, respectively

TABLE 4. Standardized Discriminant Function Coefficients

	FUNC 1	FUNC 2	FUNC 3	FUNC 4	FUNC 5
pH	-0.07780	0.39875	-0.72813	-0.28597	0.97805
D.O.	-0.15755	-0.32399	0.25823	-0.60156	-1.09422
ALKALINITY	-0.06090	-0.16229	0.36258	-0.62893	-0.05940
CONDUCTIVITY	0.25892	0.02589	0.13170	-0.19767	-0.22383
TOTAL SOLIDS	-0.43664	2.09234	0.28884	1.58946	3.10853
SUSP. SOLIDS	0.20762	-0.88644	-0.22385	-0.37946	-1.70610
TURBIDITY	0.17703	-1.60905	-0.02340	-1.76112	-1.07093
FREE CO_2	0.00197	0.00790	-0.79007	0.14661	-0.08678
DEPTH (M)	0.06194	1.25672	1.09893	-0.73320	0.44940
WIDTH (M)	0.19755	1.39467	-0.35713	-0.84978	1.01854
CURRENT	-0.01765	0.18450	0.35781	-0.67831	0.29226
TEMPERATURE	0.06749	-1.23164	0.13863	-0.43415	-0.18932
CROSS SEC. AREA	0.06456	-1.96236	-0.46527	0.69922	-1.21293
POSITION	-6.56132	51.30540	-38.94077	20.61264	15.37281
ALTITUDE	6.77611	-59.50041	43.58128	-24.48588	-15.89091
GRADIENT	-0.12318	-2.78645	2.82273	1.00519	-3.95386
STREAM ORDER	0.78970	-11.90598	8.33457	-2.24487	-4.94176
Percent of Total Variance Accounted For	30.07	12.21	11.60	8.63	7.33

(Guillory, 1981). Lists for both systems include at least 20 invaders from the Mississippi River and another 4 or 5 species localized in swamps or lower tributaries. Eighty-five species have been documented from Buffalo Bayou, but collecting efforts were concentrated in the upper and middle sections of that system (Cashner et al., 1976; Rogers et al., 1976). We assume that the species total for Buffalo Bayou would be appreciably greater than either Thompson Creek or Bayou Sara if an intensive survey of the lower reaches was conducted.

Bayou Sara is perhaps more noteworthy for the species that do not occur within the system than for those that are recorded. Poor representation of three families, Petromyzontidae, Ictaluridae, and Cyprinodontidae, is the most significant difference between the fauna of Bayou Sara and that of the two adjacent drainages. No lampreys have been taken in Bayou Sara; two species, *Ichthyomyzon gagei* and *Lampetra aepyptera,* were reported from Buffalo Bayou and one, *Ichthyomyzon gagei,* from Thompson Creek. A combined total of ten ictalurids, *Ictalurus furcatus, I. melas, I. natalis, I. nebulosus, I. punctatus, Noturus leptacanthus, N. miurus, N. nocturnus, N. phaeus,* and *Pylodicitus olivaris,* has been recorded in Thompson Creek and Buffalo Bayou, with 7 species found in each system. Although 5 catfishes, *Ictalurus furcatus, I. melas, I. natalis, I. punctatus,* and *Pylodictus olivaris* have been collected in Bayou Sara, madtoms (*Noturus*) were notably absent. Three cyprinodontids, *Fundulus catenatus, F. notatus,* and *F. olivaceus*,have been taken in Buffalo Bayou and three, *Fundulus chrysotus, F. notti,* and *F. olivaceus* have also been reported from Thompson Creek. Only one of these, *Fundulus olivaceus,* was collected in Bayou Sara. In regard to the remaining families that the three drainages share, Bayou Sara is slightly less diverse than either of its two

adjacent drainages with a composition most similar to that of Thompson Creek.

There are several plausible explanations for the lower species diversity in Bayou Sara. Bayou Sara drains an area approximately 495 km², whereas Buffalo Bayou and Thompson Creek each drain more than 800 km². This represents a significantly smaller surface area and, consequently, a smaller volume of water in Bayou Sara. Although there is not a direct correlation between habitat diversity and water volume, an increase in available habitat in terms of both extent and diversity would be expected with larger volumes of water (Hanson and Campbell, 1963; Sheldon, 1968).

Perhaps the two larger systems support more diverse faunas because of increased habitat availability. Thus Bayou Sara may lack suitable habitat or provide only marginal habitat for those species present in Buffalo Bayou and Thompson Creek that it does not share. Additionally, species extinction would be more likely in the smaller Bayou Sara system due in part to the reduction of habitat size associated with smaller volumes of water and correspondingly smaller populations of certain fish species (MacArthur and Wilson, 1967).

Lack of suitable habitat may explain the absence of such species as *Moxostoma poecilurum, Noturus phaeus* and *N. nocturnus,* which have been reported from Buffalo Bayou or Thompson Creek (Guillory, 1981). These species are typically associated with firm substrates in contrast to the shifting sand bottoms characteristic of upper Bayou Sara. Taylor (1969) reported *Noturus phaeus* to be commonly encountered under vegetation in fast flowing streams and that *N. nocturnus* avoids streams with shifting sand bottoms. Paucity of aquatic vegetation, predominance of loose sand substrates, and the absence of moderately deep, swift riffles with firm gravel substrates in Bayou Sara strongly suggest that a number of species are excluded from the system due to lack of suitable habitat.

Habitat requirements alone cannot account for the exclusion from Bayou Sara of several species including *Notorus miurus* and *N. leptacanthus* which appear in adjacent drainages. Taylor (1969) noted that *N. miurus* often occurs in lowland or base level streams with soft substrates and *N. leptacanthus* is common in riffles over sand or gravel substrates. Habitats appropriate for the above species thus appear to be available in Bayou Sara. Therefore, their absence in the system cannot be explained solely on the basis of lack of suitable habitat.

A more complex explanation of Bayou Sara's low species diversity involves environmental changes associated with the geological history of the lower Misissippi River and its tributaries. Primary consideration was given to the effects of Pleistocene glaciation on conditions in the lower Mississippi by Guillory (1978) in a discussion of modes of dispersal of upland species.

TABLE 5. Standardized Discriminant Function Coefficients from Stepwise Analysis.

	FUNC 1	FUNC 2
TEMPERATURE	-0.15230	1.05648
STREAM POSITION	0.93651	0.51216
Percent of Total Variance Accounted For	78.65	21.35

During Pleistocene interglacial periods the lower Mississippi River and associated tributaries experienced an increase in stream load, volume and deposition, followed by periodic inundations by the Gulf of Mexico. Subsequent rejuvenation of these tributary systems occurred in response to sea level lowering during glacial periods (Fisk, 1944). At these times the streams were characterized by lowered baselevels, increased gradients, clearer water and coarser sediments. Guillory (1978) suggested that glacial periods would have presented more favorable conditions for the survival and dispersal of freshwater fishes in the lower Mississippi Valley. Because periods of favorable and unfavorable conditions would have existed in all the major tributaries to the lower southeastern Mississippi River, these events would not account for existing differences in interdrainage species composition.

Recent environmental changes comparable to those mentioned above have been reported by Fisk et al. (1938). Although inundations of the lower Mississippi by the Gulf have not occurred, the meandering of the Mississippi River has produced conditions similar to those during the Pleistocene. Westward movements of the Mississippi bring about a local lengthening of its eastern tributaries, causing an overall decrease in average gradient. Eastward migrations of the river would conversely shorten these tributaries and effectively lower the baselevel. Consequently, tributaries to the eastern embayment experience gradient increases and trench their former floodplains to reach the lower baselevel (Fisk et al., 1938; Guillory, 1976).

Environmental changes associated with decrease in gradient, reduced flow, decreased oxygen tensions, increased temperature and increased siltation may have resulted in marginal, intermittent habitat for many existing species. Local extinction of species would occur if favorable habitat was not available for survival until reverse migration of the Mississippi River occurred. Guillory (1976) explained the disappearance of the blackbanded darter (*Percina nigrofasciata*) from the Thompson Creek system as a result of such recent changes. The fact that species were eliminated from Bayou Sara and not Buffalo Bayou and Thompson Creek may result from differential retention of favorable habitat during variations in the course of the Mississippi River.

Bayou Sara, Buffalo Bayou and Thompson Creek have relatively steep gradients (Fisk et al., 1938). Steep gradients in Thompson Creek and Bayou Sara result from the localized uplift along the Mobile-Tunica flexure in response to sediment overloading in the Mississippi River delta (Howe, 1936; Fisk et al., 1938). This flexure and the steepest gradient occur along a line through the headwaters of Bayou Sara. A large portion of the upstream sections of Thompson Creek and all of Buffalo Bayou lie above this line. Conceivably, some species survived unfavorable conditions occurring downstream during westward migrations of the Mississippi by moving into higher gradient sections of the tributaries. Only a small portion of the Bayou Sara system shows the high gradient associated with the Mobile-Tunica flexure. Discharge in this area is consistently low and the extreme headwaters become intermittent during dry periods. Sufficient habitat may not have been available for extended periods to support a major influx of downstream species. Therefore, elimination of species could have been more pronounced in Bayou Sara.

Intrasystem Distribution. A pattern of progressive downstream addition of species has been observed in many drainage systems (Thompson and Hunt, 1930; Burton and Odum, 1945; Kuehne, 1962; Hanson and Campbell, 1963; Larimore and Smith, 1963; Harrel et al., 1967; Jenkins and

Freeman, 1972; Whiteside and McNatt, 1972; Lotrich, 1973; Cashner and Brown, 1977; Evans and Noble, 1979; Guillory, 1981). The observed longitudinal distribution of fishes in Bayou Sara (Table 6) does not strictly follow previously described patterns. There is a progressive downstream addition of species from 1-4, reaching a high of 33 at Station 4. However, species number declines further downstream with only 28 species at Station 5 and 21 species at Station 6.

The most abundant components of the headwater fish fauna were *Nocomis leptocephalus, Notropis chrysocephalus, N. longirostris,* and *Etheostoma caeruleum.* Downstream fauna was characterized by two very abundant cyprinids, *Notropis venustus* and *Pimephales vigilax,* the addition of several species, *Hybognathus nuchalis, Notropis atherinoides* and *N. blennius,* and the presence of *Gambusia affinis.*

Among the 43 species collected during this study, only four, *Nocomis leptocephalus, Semotilus atromaculatus, Ictalurus natalis* and *Lepomis cyanellus,* were absent from lower reaches of the stream. Nineteen species were restricted to the middle and lower reaches, and 12 are continuously distributed along the main channel or are absent from only a single locality (Table 6).

All 21 species recorded at Station 1 were taken from at least one other locality. Twenty-two species were added from Stations 2-6, four at Station 3, nine at Station 4, three at Station 5 and two at Station 6. Ten species are represented by single specimens.

Variation in discharge and the associated physical and chemical changes may explain, in part, the pattern of longitudinal distribution of fishes in Bayou Sara. Extremely low flow occurred between June and December 1978. Permanent flow did persist at the six stations during this period, but many smaller tributary creeks were intermittent or dry. Hynes (1972) reported that species survive drought conditions as isolated populations in favored downstream locations, and Larimore et al. (1959) observed that the recolonization of upstream habitats occurred rapidly following restoration of flow.

Downstream displacement of species in response to low water or drought conditions would obscure any tendency for zonation and distort the pattern of species addition. Similar displacement would be expected in small creeks and tributaries to the lower reaches of Bayou Sara. Such downstream shifts may account for the infrequent occurrence of *Erimyzon oblongus, Etheostoma caeruleum, E. whipplei,* and *Percina ouachitae* at Stations 5 and 6 and *Nocomis leptocephalus, Semotilus atromaculatus* and *Ictalurus natalis* at Station 4.

C. Data Analysis

Multiple discriminant functions analysis was employed to assess the importance of 17 environmental variables in regard to spatial separation of the groups (species) in Bayou Sara. Seventeen discriminant functions (DF) were extracted during the direct analysis. Standardized DF coefficients for each of the 17 variables in these functions (Table 4) indicate the dominance of two factors, altitude and stream position.

The high positive coefficient for gradient in DF I, in conjunction with the prominant negative one for stream position, indicates a marked restriction of species to the headwaters and lower reaches of Bayou Sara. According to the analysis, the downstream variation in altitude and stream position accounts for the longitudinal variation in species distribution in the Bayou Sara system. Because, however, the 17 DF extracted during the direct analysis failed to reach a high degree of statistical significance ($p > .10$), sufficient variation between species apparently does not exist in these two variables and the other 15 parameters to account for the observed species separations.

TABLE 6. Longitudinal Distribution of Fishes in Bayou Sara. Line is continuous if a species was not missing from one or more successive localities, otherwise the line is dashed.

STATION	CODE	1	2	3	4	5	6
Lepomis cyanellus	32	———	- - - -	———	———		
Ictalurus natalis	26	———	———	———	———		
Semotilus atromaculatus	22	———	———	———	———		
Nocomis leptocephalus	9	———	———	———	———		
Micropterus salmoides	36	———	- - - -	- - - -	- - - -	———	———
Erimyzon oblongus	24	———	- - - -	———	- - - -	———	———
Micropterus punctulatus	35	———	- - - -	———	- - - -	———	———
Fundulus olivaceus	28	———	———	———	———	———	———
Notemigonus crysoleucas	10	———	———	- - - -	———	———	———
Etheostoma whipplei	41	———	- - - -	- - - -	- - - -	- - - -	———
E. caeruleum	40	———	———	———	———	- - - -	———
Percina ouachitae	42	———	———	———	———	- - - -	———
Pimephales notatus	20	———	———	———	———	———	———
Carpiodes carpio	23	———	———	———	———	———	———
Notropis chrysocephalus	14	———	———	———	———	———	———
N. longirostris	15	———	———	———	———	———	———
N. venustus	18	———	———	———	———	———	———
N. volucellus	19	———	———	———	———	———	———
Gambusia affinis	29	———	———	———	———	———	———

TABLE 6 CONT.

STATION	CODE	1	2	3	4	5	6
Lepomis macrochirus	33						
L. megalotis	34						
Pimephales vigilax	21						
Ictalurus punctatus	37						
Notropis lutrensis	16						
Pomoxis annularis	37						
Notropis umbratilis	17						
Lepisosteus oculatus	1						
Dorosoma cepedianum	3						
Ictiobus bubalus	25						
Pomoxis nigromaculatus	38						
Hybognathus nuchalis	6						
Notropis atherinoides	11						
N. blennius	12						
Aplodinotus grunniens	43						
Notropis camurus	13						
Cyprinus carpio	5						
Labidesthes sicculus	30						
Dorosoma petenese	4						
Lepisosteus platostomus	2						
Elassoma zonatum	39						
Morone chrysops	31						
Hybopsis aestivalis	7						
H. storeriana	8						

Similar results were obtained with the stepwise DF analysis, with stream position and temperature selected for inclusion into the analysis. One statistically significant ($p<0.01$) DF, accounting for 78.7% of the among-species variance, was extracted during the stepwise analysis. As was the case in the direct analysis, stream position provided the most significant contribution to the formulation of this function. The high positive standardized coefficient for this variable (Table 5) indicates once again a distinct separation of species at upstream localities. The negative coefficient for temperature signifies species separation in the cooler waters of the upstream stations. However, the magnitude of the coefficient for temperature indicates a minor contribution to this function.

Discriminant functions scores for each of the 33 species were also computed during the analysis. These scores were based on physical and chemical measurements associated with the time of capture of each species. A discriminant score is thus obtained for a species for each instance it was collected. Mean discriminant scores were tabulated to facilitate evaluation of species distribution in relation to important environmental variables. Large discriminant scores indicate the presence of a species where significant environmental variables of that function are also correspondingly large or small depending on the signs of the DF coefficients (Nie et al., 1975).

Figure 3 is a plot of the mean discriminant scores for 33 species on DF I of the stepwise analysis. The underlined numbers correspond to one of the 43 species collected during this study. A key to the species codes appears in Table 6. The distribution of mean discriminant scores (Fig. 3) appears to corroborate the observed pattern of longitudinal distribution of species in Bayou Sara (Table 6). Three species, *Semotilus atromaculatus* (22), *Erimyzon oblongus* (23), and *Etheostoma caeruleum* (40), were restricted to upstream areas where water temperatures were the lowest. Although not restricted to the most upstream stations, two species, *Nocomis leptocephalus* (9) and *Ictalurus natalis* (26), appear to have been limited to more upstream localities with cooler water temperatures. A large number of species were either restricted to the mid-stream sections of Bayou Sara or were continuously distributed along the watercourse ($-0.5<DS<+0.5$). Furthermore, a number of species had their distribution limited to the lower reaches where water temperatures were the highest.

Results of both the direct and stepwise DF analyses are consistent with the findings of Sobczak (1976) and Rogers, et al. (1976). Physical measurements of mean depth, cross-sectional area, stream position and altitude were the most significant environmental factors contributing to separation of species in Bayou Lacombe, Louisiana (Sobczak, 1976). Rogers et al. (1976) found stream depth, width and alkalinity to be the most important factors accounting for variance among intrasystem distributions in Buffalo Bayou, Mississippi.

One reason for the dominance of physical factors in separating species distributions in these two studies and especially Bayou Sara can be postulated. The range of variation within the stream systems, relative to the fishes' ranges of tolerance, may be smaller for the chemical factors than for the physical factors. Physical measurements would therefore, assume more importance in determining the distribution of species that are not adversely affected by the range of chemical conditions encountered in each of these streams.

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PLANTS AND PLANT COMMUNITIES OF JEAN LAFITTE NATIONAL HISTORICAL PARK, LOUISIANA.

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ABSTRACT

The 3240 hectare Barataria Unit (core area) of Jean Lafitte National Historical Park in southeastern Louisiana was surveyed phytosociologically and floristically. The park area has a wide range of natural habitats which were classified as marsh, cypress-tupelo swamp, intermediate swamp, and hardwood bottoms. The three forest types were analyzed by the point-quarter method to compare plant composition by differences in importance values. The hardwood bottoms are dominated by *Quercus nigra,* with *Liquidambar styraciflua, Celtis laevigata,* and *Quercus virginiana* as subdominants, while the cypress-tupelo swamp typically supports *Taxodium distichum, Nyssa aquatica* and *Fraxinus profunda.* The intermediate swamp supports species characteristic of both hardwood bottoms and cypress-tupelo swamps. The marsh habitat is quite diverse, the characteristically dominant species being *Sagittaria lancifolia, Persecaria punctata, Typha* spp., and *Eleocharis* spp.; *Spartina patens* dominates some areas. Aquatic and man-altered environments are described qualitatively. A checklist of vascular plants comprising 328 species in 88 families is included. No endangered or threatened species were found.

INTRODUCTION

The nation's newest national park, Jean Lafitte National Historical Park, was established in 1978 "in order to preserve for the education, inspiration and benefit of present and future generations significant examples of natural and historical resources of the Mississippi Delta region and to provide for their interpretation in such manner as to portray the development of cultural diversity in the region . . ." (U.S. Congress, Public Law 95-625, 1978). The park is unique in that it consists of a Barataria Unit of largely undisturbed vegetation and a number of "extended area units" of historical or cultural interest such as plantation houses, fortifications, and museums, all within the Mississippi Delta region. The Barataria Unit located ten miles south of New Orleans is itself divided into two areas, a "core area" of roughly 8,000 acres (3240 hectares) and an adjacent northern "park protection zone" of about 11,400 acres (4610 hectares). The present study is a baseline description of the plants and plant communities of the core area.

Study Area.

The core area of the Jean Lafitte National Historical Park is in Jefferson Parish on the southern border of the New Orleans metropolitan area. Its boundaries are irregular (Fig. 1). The western border is the shore of Lake Salvador, whereas the area is bounded on the south by bayous Barataria and Villars and on the east by Louisiana Highway 3134. The northeastern boundary is a hurricane protection levee and canal adjacent to zoned developed land, a part of greater New Orleans. The northern border is the edge of marshland that forms the park protection zone.

The core area is located midway on the

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eastern edge of the 400,000 hectare (990,000 acre) Barataria Basin (Fig. 2). Various ecological studies within the basin have been published in recent years (Conner & Day, 1976; Hopkinson et al., 1978; Day et al., 1973; Kirby & Gosselink, 1976). The basin is approximately 80 miles (129 km) long, with Lake Des Allemands near its headwaters and the Gulf of Mexico at its southern terminus. Several large, shallow lakes are encompassed by it. The lakes are interconnected by bayous and surrounded by extensive marshland which in turn is bordered by higher ground.

The eastern third of the core area is such an area of higher elevation bisected by Bayou des Familles. The high ground developed thousands of years ago from silt deposition when the bayou was an active distributary of the Mississippi River. The highest land (elevation about one meter m.s.l.) in the park is this natural ridge; east

Figure 2. Map of southeastern Louisiana showing extent of the Barataria Basin and locality of core area.

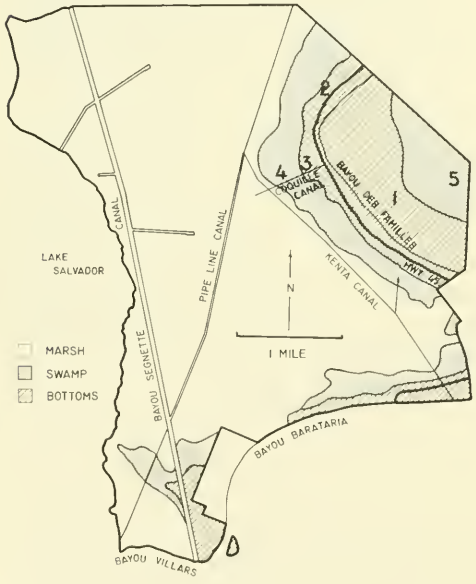

Figure 1. Map of core area, Barataria Unit, Jean Lafitte National Historical Park, showing distribution of major plant communities and location of the five study sites.

and west of it the elevation gradually declines until swamp and marsh is reached. Such elevational changes lead to the development of distinctively different plant communities within the study area.

Near and away from the Bayou des Familles is one of the southern-most bottomland forests in the United States. Man has not logged these during the last 50 to 75 years, although exact dates could not be verified (Norgress, 1936; Mancil, 1972). According to the classification of Braun (1950), two bottomland forest types are in the park. A "hardwood bottoms" community occurs on the highest land along both shores of Bayou des Familles, whereas "cypress-tupelo forests" occur east and west of the bottoms, also paralleling the bayou but on slightly lower ground. Between these two forest types is an intermediate swamp.

The park's western two-thirds is a marshland lying within the Barataria Basin. It is transected in several places by man-made canals and once by a high tension power-

line. The Bayou Segnette Canal has numerous hunting, fishing, and weekend retreat camps along its shores, but the other canals have been largely untouched since construction.

Soils.

The core area has two distinct classes of soils. The eastern third has alluvial soils of the Inceptisols type supportive of hardwood bottom vegetation. The marsh vegetation in the western region grows in saturated peat and muck soils or Histosols. After winter and early spring rains, most Inceptisols remain saturated for weeks and even months in areas transitional to the marsh.

Climate.

The park is located in the subtropics where weather is strongly influenced by the close proximity of the Gulf of Mexico. Rainfall exceeds 160 cm (64 inches) annually, highest rainfall being in August and September. October is the driest month of the year. The mean annual temperature is approximately 21 °C (70 °F), ranging from a mean low in January of 11 °C (52 °F) to a July average of about 29 °C (84 °F). The growing season is in excess of 260 days.

Methods

Over the course of two years the flora of Lafitte Park's core area was studied floristically and phytosociologically. Standard collecting and preparation techniques were employed in accumulating herbarium specimens to document the occurrence of plant species. More than twenty visits were made and all habitats studied, most more than once and at different seasons. Voucher specimens are deposited in the Tulane University Herbarium, although not all species are represented by specimens; when plants were found in a sterile condition, but identifiable in the field, no material was collected. This was especially the case for many trees and some aquatics.

Color infrared photographs were used to delimit plant communities within the park. Five general types of communities were found: (1) hardwood bottom, (2) intermediate swamp, (3) cypress-tupelo swamp, (4) marsh, and (5) man-altered. Open bodies of water support additional hydric communities. The bottomland forests were quantitatively sampled using 25 point-quarters (Cottam & Curtis, 1956; Cox, 1976) at each of five sites (Fig. 1). Two sites located 1.6 km apart were in hardwood bottoms on opposite ridges of Bayou des Familles. Two sites were in cypress-tupelo swamps also on opposite sides of and farther from the bayou. The final site was in an intermediate swamp. At all sites, species importance values were calculated using relative density and dominance values. Only woody plants with a stem diameter larger than 6 cm. at breast height were measured. The marsh, aquatic, and altered areas were studied qualitatively; i.e. estimates were made of species importance.

Results

1. Description of plant communities.

An important environmental parameter controlling the distribution and composition of plant communities in the Lafitte Park is elevation of the land, which affects soil saturation and hydroperiod. Elevational differences of only a few centimeters result in striking changes in vegetation. Many thousands of acres of Louisiana are saltwater marshland, but salt intrusion is but a minor factor in the park, only minimally penetrating as far as southern Lake Salvador where tides are weak.

A. Hardwood bottoms. The hardwood bottom forests along Bayou des Familles comprise 437 hectares (1080 acres) of the 3240 hectare core area in the Barataria Unit and are dominated by water oak (*Quercus nigra*) (Fig. 3). Subdominants within these ridge forests include sweet gum (*Liquidambar styraciflua*), hackberry (*Celtis laevigata*), and live oak (*Quercus virginiana*). From the two hardwood bot-

tom sites sampled, the average importance value (AIV) of each dominant and subdominant species mentioned above was 82, 33, 31, and 20 respectively (Tables 1 & 2). Such a species composition agrees with Braun's (1950) description of bottoms in the Mississippi Delta region. Also, as she states, "the southern aspect of this forest is emphasized by the abundant palmetto (*Sabal minor*)." Several other species that characterize these forests include box-elder (*Acer negundo*), honey-locust (*Gleditsia triacanthos*), American elm (*Ulmus americana*), and Nuttall oak (*Quercus nuttallii*).

The most common shrub species in the hardwood bottoms are palmetto and green haw (*Crataegus viridis*). In some areas thickets of possum-haw (*Ilex decidua*) are found. Forest gaps support elderberry (*Sambucus canadensis*) and French-mulberry (*Callicarpa americana*). Occasionally the introduced camphor-tree (*Cinnamomum camphora*) is found. Vines are quite striking and common, including poison-ivy (*Rhus toxicodendron* var. *vulgaris*), Virginia creeper (*Parthenocissus quinquefolia*), supple-jack (*Berchemia scandens*), pepper-vine (*Ampelopsis arborea*), muscadine (*Vitis rotundifolia*), and hemp-weed (*Mikania scandens*).

Penfound and Howard (1940) reported results from a phytosociological study of a similar forest along an abandoned distributary located approximately 30 miles northeast of our study site. They found the dominant species to be water oak and live oak, with hackberry as the only important subdominant. Although sweet gums were not recorded there, several of the minor species are common to their study area and the Lafitte Park. Site differences probably result from local differences in seed recruitment.

B. Swamps. Lafitte Park has 445 hectares

Figure 3. Hardwood bottom forest near site 1 in late autumn.

(1100 acres) of cypress-tupelo swamps. This community near the level of neighboring marshes is dominated by bald cypress (*Taxodium distichum,* AIV = 129) in areas where water level fluctuations have permitted re-establishment after logging (Fig. 4). Water tupelo (*Nyssa aquatica* AIV = 38) is often a sub- or co-dominant. Other sub-dominants are swamp red maple (*Acer rubrum* var. *drummondii,* AIV = 25) and ashes (*Fraxinus* spp., AIV = 24) (Tables 3 & 4). Shrubs within these swamps include wax-myrtle (*Myrica cerifera*) and button-bush (*Cephalanthus occidentalis*). Here, the vines are cat-briar (*Smilax* spp.), trumpet-creeper (*Campsis radicans*), and poison-ivy.

Hall and Penfound (1939) studied a similar swamp forest located 45 miles northeast of Lafitte Park; Montz and Cherubini (1973) described an extensive, although less typical swamp with only one overstory species, bald cypress. Such anomalies probably result from differences in seed recruitment and germination.

In contrast to hardwood bottoms, the swamp forests have herbaceous ground cover. Some of the herbs are smart-weed (*Persicaria punctata*), alligator-weed (*Alternanthera philoxeroides*), swamp-potato (*Sagittaria lancifolia*), and water-hyacinth (*Eichhornia crassipes*). During the spring, patches of red iris (*Iris fulva*) and giant blue iris (*Iris giganticaerulea*) can be quite attractive beneath cypress laden with spanish-moss (*Tillandsia usneoides*); in the autumn the sunlit border swamps are covered yellow with bur-marigold (*Bidens laevis*).

The number of different species in the hardwood bottom forest is higher (richness = 9) than in the wetter swamp forests (richness = 5), probably because of the governing influence of water on germination and growth. Forests intermediate in elevation, i.e., those slightly less mesic than the hardwood bottoms, have the greatest number of species (richness = 14; Table 5). In Lafitte Park, the intermediate swamp occurs at an elevation between that of hardwood bottom and cypress-tupelo areas. Such intermediate swamp may be quite extensive due to gradual slope. Characteristically there is an abundance of swamp red maple, small American elms, and water oaks (Table 5). A few bald cypress can be found among the many other tree species. Here the palmetto understory is quite dense, often impenetrable, with plants up to 2 m. tall. A forest of this intermediate type and a wetter swamp forest in the upper drainage

TABLE 1. Importance values for trees in hardwood bottom--site 1.

Species	Number	Average Basal Area	Density/m^2	Relative Density	Dominance	Relative Dominance	Importance Value
Quercus nigra	47	385	0.034	47	13.1	32.9	79.9
Liquidambar styraciflua	14	640	0.010	14	6.5	16.3	30.3
Celtis laevigata	19	328	0.014	19	4.5	11.3	30.3
Quercus virginiana	2	8627	0.001	2	12.1	30.4	32.4
Acer negundo	4	130	0.003	4	0.4	1.0	5.0
Acer rubrum var. drummondii	1	350	0.001	1	0.2	0.6	1.6
Ulmus americana	10	215	0.007	10	1.6	3.9	13.9
Gleditisia triacanthos	1	2003	0.001	1	1.4	3.5	4.5
Cinnamomum camphora	2	29	0.001	2	0.1	0.1	2.1

TABLE 2. Importance values for trees in hardwood bottom--site 2.

Species	Number	Average Basal Area	Density/m^2	Relative Density	Dominance	Relative Dominance	Importance Value
Quercus nigra	16	2771	0.038	16	107.2	67.9	83.9
Liquidambar styraciflua	22	413	0.057	22	22.1	14.0	36.0
Celtis laevigata	24	195	0.051	24	11.3	7.2	31.2
Quercus virginiana	2	1899	0.004	2	9.1	5.8	7.8
Acer negundo	16	66	0.043	16	2.6	1.6	17.6
Acer rubrum var. drummondii	5	202	0.014	5	2.4	1.5	6.5
Ulmus americana	4	96	0.011	4	0.9	0.6	4.6
Ulmus rubra	10	88	0.023	10	2.1	1.3	11.3
Crataegus viridis	1	29	0.002	1	0.1	0.1	1.0

of the Barataria Basin were studied by Conner and Day (1976). Their species list compared with the one we compiled of species growing in similar environments demonstrates the relative homogeneity of these forest types in southern Louisiana.

C. Marsh. Ecologically a marsh is distinguished from a swamp by the lack of trees. Marsh is the largest community type within the Lafitte Park, covering approximately 2405 hectares (5945 acres). These areas of peat and muck soils have an elevation of less than one meter (m.s.l.), close to the level of Lake Salvador on which they border. Most of the marsh is sustained by trapped or slowly draining rainwater and contains diverse species of freshwater herbs. However, the occasional influx of slightly saline water from the lower Barataria Basin has resulted in a small marsh of somewhat different species composition along the southeastern shore of Lake Salvador to the Bayou Segnette Canal (Fig. 5B). Brackish water does not penetrate beyond the levees of the canal. Penfound and Hathaway (1938) studied this same locality and called it a brackish marsh, although it is now more correctly labeled intermediate marsh (Chabreck, 1972). The region can be distinguished from the freshwater marsh by

TABLE 3. Importance values for trees in swamp--site 4

Species	Number	Average Basal Area	Density/m^2	Relative Density	Dominance	Relative Dominance	Importance Value
Taxodium distichum	31	1211	0.020	31	24.2	69.6	100.6
Nyssa aquatica	20	473	0.013	20	6.1	17.7	37.7
Acer rubrum var. drummondii	20	123	0.013	20	1.6	4.6	24.6
Fraxinus profunda	19	192	0.012	19	2.3	6.6	25.6
Liquidambar styraciflua	6	85	0.004	6	0.3	1.0	7.0
Myrica cerifera	4	53	0.003	4	0.2	0.4	4.4

the dominance of cord grass (*Spartina patens*). Common species along the lake shore are swamp-potato (*Sagittaria lancifolia*), salt-marsh mallow (*Kosteletzkya virginica*), and seaside goldenrod (*Solidago sempervirens*).

In the freshwater marsh (Fig. 5A), swamp-potato is ubiquitous, covering at least sixty percent of the area. Occasionally the species occurs in pure stands, but more commonly it is mixed with other associates, such as smart-weed (*Persicaria* spp.) and alligator-weed. The diversity within the marsh community can best be described by identifying those plant associations which are several hectares or just a few hundred square meters in area; in any one area the association may be as described below or mixed with other less common species.

Wax-myrtle "islands" are scattered in the northern and eastern portions of the marsh (Fig. 5A). Larger stands of this evergreen shrub shade a dense and homogeneous ground cover of spike-rush (*Eleocharis* sp.). The myrtle islands seem to float on the marsh inasmuch as jumping on them makes the entire island undulate.

Other distinct marshland associations of limited size include stands of wild-rice (*Zizaniopsis miliacea*) in the southeastern marsh. Scattered throughout the eastern marsh are massive sedge communities which include giant bulrush (*Scirpus californicus*), several species of spike-rush, and flat sedge (*Cyperus* spp.). Cat-tails (*Typha* spp.) grow throughout the marsh, and in several places occur in very large stands. Panic grass (*Panicum* spp.) is scattered throughout and may form nearly pure stands (particularly *P. commutatum*). In places saw-grass (*Cladium jamaicense*) may be associated with any of the above species.

Figure 4. Bald cypress in swamp forest at site 5 in early spring.

TABLE 4. Importance values of trees in swamp--site 5.

Species	Number	Average Basal Area	Density/m^2	Relative Density	Dominance	Relative Dominance	Importance Value
Taxodium distichum	63	1245	0.036	63	33.0	94.0	157.0
Acer rubrum var. drummondii	13	168	0.007	13	1.3	3.6	16.6
Fraxinus profunda	20	75	0.012	20	0.7	1.9	21.9
Liquidambar styraciflua	1	154	0.001	1	0.1	0.3	1.3
Myrica cerifera	3	51	0.002	3	0.1	0.2	3.2

D. Aquatic community. Except for rare small pools of water in the marsh, the only aquatic habitats are those of man-made canals, approximately 117 hectares (290 acres) of them (Fig. 6A). Canals were dug at widely different times spanning a period of fifty years, and thus are in varying states of their natural reversion to marshland. Coquille Canal is the oldest, and Bayou Segnette Canal the youngest; these differences in age are reflected in species composition. Plant communities in shallow, older canals have great diversity and density, even choking the canal, whereas younger, deeper canals have fewer species and much open water. Water-hyacinth, alligator-weed, and duck-weed (*Lemna* spp.) are very common floating and rooted-emergent aquatics. Fanwort (*Cabomba caroliniana*), coon-tail (*Ceratophyllum demersum*), and water-nymph (*Najas guadalupensis*) are the most common submerged aquatics.

E. Altered communities. The activities of

TABLE 5. Importance values for trees in transition forest--site 3.

**Fraxinus profunda* and *F. pensylvanica* were sterile at the time of the survey and not distinguishable.

Species	Number	Average Basal Area	Density/m^2	Relative Density	Dominance	Relative Dominance	Importance Value
Acer rubrum var. drummondii	32	217	0.030	32	6.5	22.3	54.3
Ulmus americana	18	396	0.016	18	6.3	21.7	38.7
Quercus nigra	17	306	0.016	17	4.9	16.8	33.8
Liquidambar styraciflua	5	695	0.005	5	3.5	11.9	16.9
Quercus nuttallii	5	534	0.005	5	2.7	9.2	14.2
Quercus virginiana	5	470	0.005	5	2.4	8.1	13.1
*Fraxinus spp.**	7	229	0.007	7	1.6	5.4	12.4
Celtis laevigata	4	188	0.004	4	0.8	2.5	6.5
Crataegus viridis	2	70	0.002	2	0.1	0.5	2.5
Acer negundo	2	65	0.002	2	0.1	0.4	2.4
Taxodium distichum	1	255	0.001	1	0.3	0.8	1.8
Ilex decidua	1	34	0.001	1	0.1	0.1	1.1
Cornus drummondii	1	29	0.001	1	0.1	0.1	1.1

man have created several artificial communities within the Lafitte Park. The fact that some of these communities continue to be disturbed and others not enabled us to divide them into two categories based on their histories and present vegetation. In one instance the communities undergo succession toward compositions characteristic of their elevation and hydroperiod. Spoilbanks along shores of canals are such communities; not only do these artificial levees show successional transition from herbaceous vegetation to hardwoods, but there is a later succession to marshland as the spoilbank gradually subsides. An example of these stages in levee succession is found along the more than 80 year old Kenta Canal. The northern and extreme southern banks are covered with beautiful live oaks, sweet gums, and hackberries (Fig. 6A), a good example of late spoil succession and reminiscent of chenieres in southern Louisiana. In contrast, the central banks have further subsided nearly to the level of the surrounding marsh and here are found red bay (*Persea borbonia*), wax-myrtle, swamp red maple, and marsh-elder (*Iva annua*). As subsidence continues the woody plants will be replaced by herbaceous species now found in the marsh.

The youngest and driest spoilbanks along southern Bayou Segnette Canal and associated spur canals support a different vegetation dominated by roseau-cane (*Phragmites australis*), black willow (*Salix nigra*), goldenrod (*Solidago altissima*), and dewberry (*Rubus trivialis*) (Fig. 6B). The northern portions of Bayou Segnette Canal are unique in having pure stands of the introduced and weedy Chinese tallow-tree (*Sapium sebiferum*) (Fig. 5B).

The other type of altered community is that which is continuously disturbed by man, i.e., succession is prevented from following its normal course. Within Lafitte Park such areas include roadsides, powerline right-of-ways, and various commercial and industrial border areas. Here grow the same weedy plants found on young spoil, particularly thickets of dewberry, scattered black willow, seedlings of nearby forest species, various grasses, and numerous fall-flowering annuals such as asters, goldenrods, and other members of the composite family.

2. Floristic inventory.

The results of our floristic inventory of the core area of the Jean Lafitte National Historical Park are presented in the Appendix where 328 species of vascular plants are listed. Table 6 shows the distribution of species among the major plant groups including those families of flowering plants with the largest number of species in the park. The sequence of plant families and the botanical names used in the Appendix generally follow Correll and Johnston (1970); within each family the genera and species are arranged alphabetically. Common names are those believed to be in use in southern Louisiana, but different names may be applied in other parts of the country. A general statement following each name identifies the habitat in which the species was observed to be growing within the study area, although other habitats may be occupied by any species in other parts of its range.

The flora of Louisiana is not especially well known or documented when compared with that of our more northern states. Indeed, there is no modern published Flora which covers the entire state. Although a new Flora of the southeastern United States is in preparation, only the volume treating the composite family has been published thus far (Cronquist, 1980). Manuals covering other states with similar floras have proved most useful in the identification of our plant materials, particularly those of Radford et al. (1964) and Correll and Johnston (1970). Some more detailed studies of Louisiana plant groups are also available,

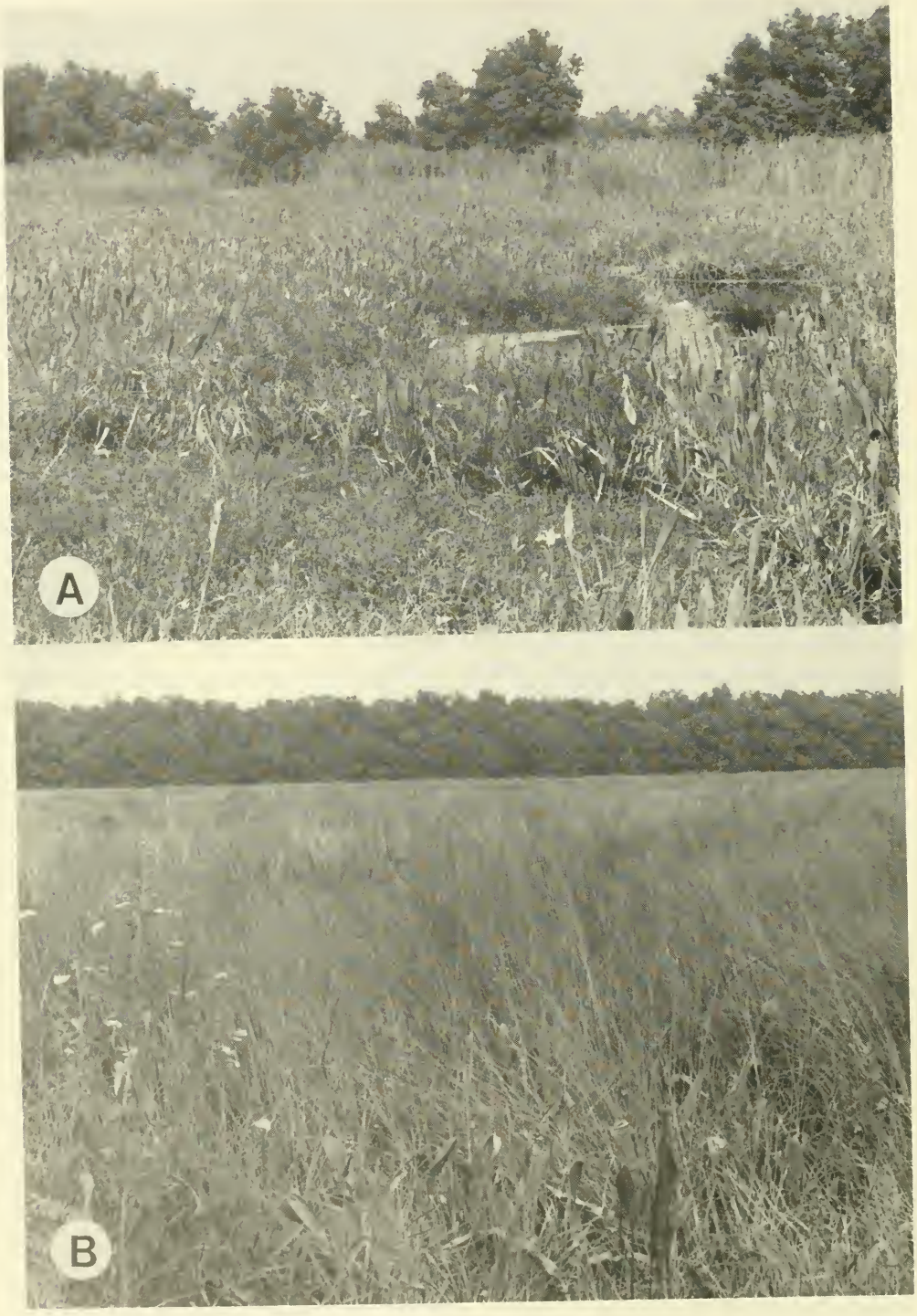

Figure 5. A: Freshwater marsh near Bayou Segnette Canal dominated by smart-weed and swamp-potato with islands of wax-myrtle in background. B: Intermediate marsh near shore of Lake Salvador dominated by cord grass with swamp-potato and salt-marsh mallow near shore; Chinese tallow-trees on spoilbank visible in rear.

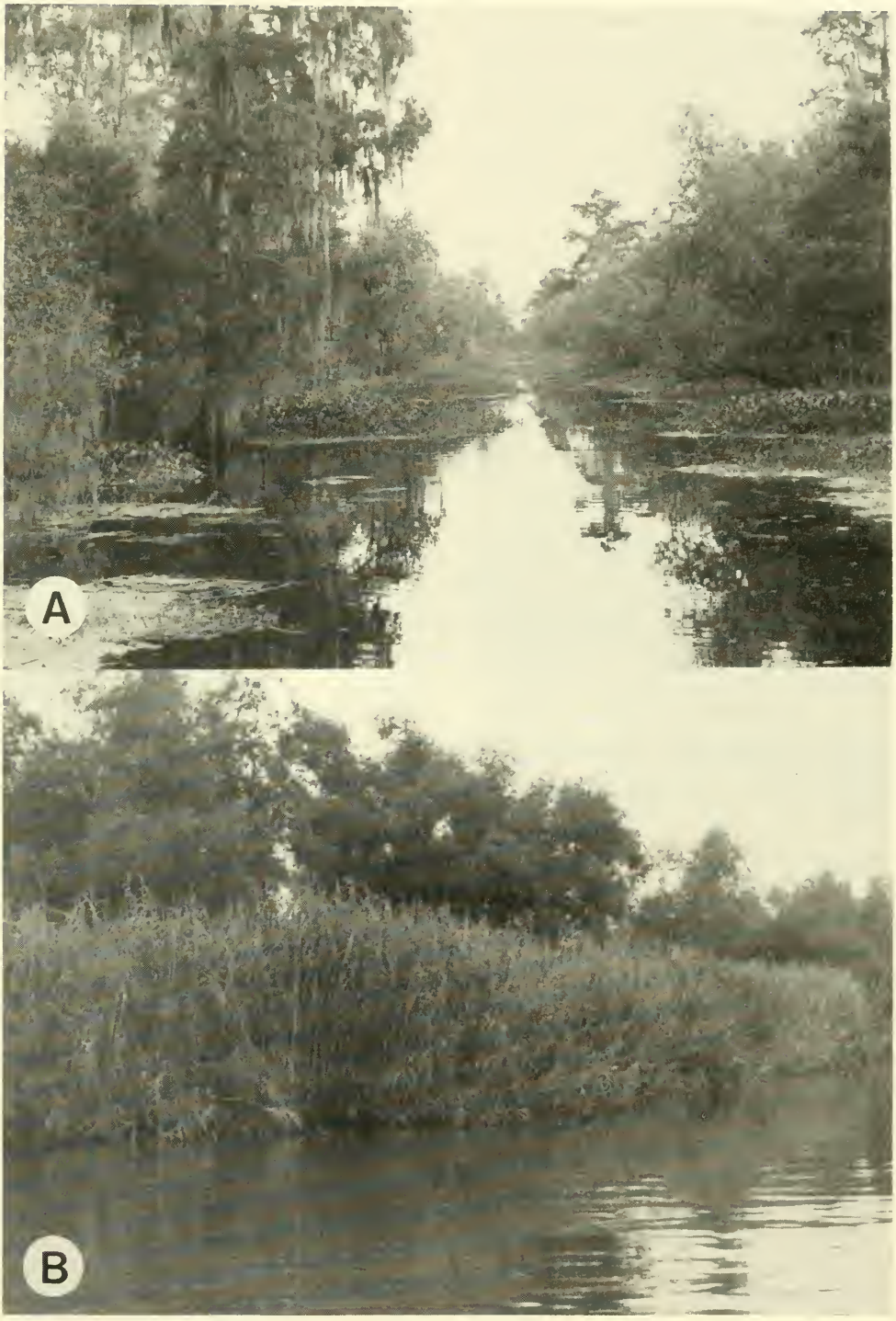

Figure 6. A: Kenta Canal showing water-hyacinth, alligator-weed, and duck-weed, bordered by mature spoil vegetation. B: Young spoil with black willow and roseau-cane along Bayou Segnette Canal.

e.g., those of Leguminosae (Lasseigne, 1973) and Gramineae (Allen, 1980), and they were consulted frequently. Other publications treat the aquatic vegetation of our area (Godfrey & Wooten, 1979, 1981), and checklists may supply valuable nomenclatural information (Thieret, 1972a, 1972b; Thomas & Allen, 1982).

Although we believe that our species inventory is substantially complete, no such list can ever be final. Aside from species that may have been overlooked, the vagility of plants suggests that various species may appear in the Lafitte Park as suitable habitats become available. Studying the vegetation near Bayou Villars in 1938, Penfound and Hathaway recorded the following plant species which we have not yet encountered in the study area: *Aster tenuifolius* L., *Calystegia sepium* (L.) R. Br. (*Convolvulus repens* L.), *Eleocharis albida* Torr., *Eleocharis montana* (HBK) R. & S. (*E. nodulosa* (Roth) Schultes), *Fimbristylis castanea* (Michx.) Vahl, *Iva frutescens* L., *Leptochloa fascicularis* (Lam.) Gray, *Lythrum lineare* L., *Paspalum vaginatum* Sw., *Scirpus olneyi* E. & G., and *Scirpus validus* Vahl. Any of the above species may be discovered within the Lafitte Park as the area continues to be explored botanically. Likewise, Montz (1980) has recorded the distribution of many aquatic plants in Louisiana. The following commonly occurring species which he records from Jefferson Parish have yet to be found within the park boundaries: *Myriophyllum brasiliensis* Camb., *Utricularia biflora* Lam., and *Zannichellia palustris* L. Similarly, we did not discover any species of *Wolffiella,* although they are common in waterways of the state.

No endangered or threatened plant species were encountered in the Lafitte Park, although some species are only occasional or rare, particularly *Asclepias perennis, Spiranthes cernua* var. *odorata, Habenaria repens,* and *Iris fulva.* Some woody plants which are rare in the park, such as species of *Citrus,* have escaped from cultivation. In general, however, the species found in the core area are representative of the southern Louisiana flora and the habitats that they occupy.

Table 6. Major taxa present.

Taxon	*No. of species*
Pteridophyta:	5
Gymnospermae:	1
Angiospermae:	
Monocotyledonae:	
Gramineae:	37
Cyperaceae:	26
other families:	36
Dicotyledonae:	
Compositae:	33
Leguminosae:	21
Polygonaceae:	10
Euphorbiaceae:	8
Scrophulariaceae:	8
Umbelliferae:	8
other families:	135
Total:	328

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Appendix
Checklist of Vascular Plants

PTERIDOPHYTA

Schizaeaceae

Lygodium japonicum (Thunb.) Sw. CLIMBING FERN

Climbing over trailside and roadside vegetation

Salviniaceae

Azolla caroliniana Willd. WATER FERN

Floating aquatic in swamps

Polypodiaceae

Asplenium platyneuron (L.) D. C. Eat. EBONY SPLEENWORT
Shaded hardwood bottoms
Polypodium polypodioides (L.) Watt. RESURRECTION FERN
Epiphyte, mostly on oaks
Thelypteris kunthii (Desv.) Morton SOUTHERN SHIELD FERN
Shaded hardwood bottoms

GYMNOSPERMAE

Taxodiaceae

Taxodium distichum (L.) Rich. BALD CYPRESS, CIPRE, CYPRES
Wet swampland

ANGIOSPERMAE

Typhaceae

Typha domingensis Pers. CAT-TAIL
Marshes and wet depressions
Typha latifolia L. COMMON CAT-TAIL
Marshes and wet depressions

Najadaceae

Najas guadalupensis (Spreng.) Magnus COMMON WATER-NYMPH
Submerged aquatic

Alismataceae

Echinodorus cordifolius (L.) Griseb. CREEPING BURHEAD, HERBE À MALO
Swamps
Sagittaria lancifolia L. SWAMP-POTATO
Marshes and wet depressions
Sagittaria platyphylla Engelm. SWAMP-POTATO
Swamps

Hydrocharitaceae

Limnobium spongia (Bosc.) Steud. FROG'S-BIT
Floating aquatic

Gramineae

Andropogon glomeratus (Walt.) BSP.
Open roadsides
Arthraxon hispidus (Thunb.) Makino
Disturbed areas
Digitaria ischaemum (Schreb.) Schreb. CRAB GRASS
Disturbed areas
Digitaria sanguinalis (L.) Scop. CRAB GRASS
Disturbed areas
Echinochloa crusgalli (L.) Beauv. BARNYARD GRASS
Disturbed areas
Echinochloa walteri (Pursh) Heller
Marshes
Eleusine indica (L.) Gaertn. GOOSE GRASS
Open areas

Elymus virginicus L. WILD RYE
Disturbed areas
Erianthus giganteus (Walt.) Muhl. PLUME GRASS
Open roadsides
Hordeum pusillum Nutt. LITTLE BARLEY
Open fields and roadsides
Leersia lenticularis Michx. CUT GRASS
Marshes
Leersia virginica Willd. WHITE GRASS
Roadsides
Oplismenus hirtellus (L.) Beauv.
Open areas and shaded woods
Panicum anceps Michx. PANIC GRASS
Open roadsides
Panicum commutatum Schult. PANIC GRASS
Open areas
Panicum dichotomiflorum Michx. FALL PANIC
Open areas
Panicum gymnocarpon Ell. PANIC GRASS, SWAMP PANIC
Marshes and open areas
Panicum hemitomon Schult. MAIDEN-CANE
Marshes
Panicum rigidulum Nees PANIC GRASS
Open areas
Panicum virgatum L. PANIC GRASS, FEATHER GRASS
Open areas
Paspalum distichum L. KNOT GRASS
Roadsides
Paspalum urvillei Steud. VASEY GRASS
Open areas, roadsides
Phalaris caroliniana Walt. CANARY GRASS
Open areas
Phragmites australis (Cav.) Trin. ex Steud. ROSEAU-CANE
Wet depressions, marsh edges
Poa annua L. BLUE GRASS
Roadsides
Polypogon monspeliensis (L.) Desf. RABBIT-FOOT GRASS
Roadsides
Sacciolepis striata (L.) Nash
Marshes
Setaria geniculata (Lam.) Beauv. BRISTLE GRASS
Disturbed areas
Setaria glauca (L.) Beauv. YELLOW FOX-TAIL
Open roadsides
Setaria magna Griseb. GIANT FOX-TAIL
Disturbed areas

Spartina cynosuroides (L.) Roth QUILL-CANE
Marsh edges and spoilbanks
Spartina patens (Ait.) Muhl. CORD GRASS, COUCH GRASS, WIRE GRASS
Marshes
Sphenopholis obtusata (Michx.) Scribn. WEDGE GRASS
Trailsides in hardwood bottoms
Sporobolus indicus (L.) R. Br. SMUT GRASS
Roadsides
Stenotaphrum secundatum (Walt.) Ktze. ST. AUGUSTINE GRASS
Disturbed areas
Trisetum pensylvanicum (L.) Beauv. ex R. & S.
Open areas
Zizaniopsis miliacea (Michx.) Doell. & Asch. SOUTHERN WILD-RICE
Marshes

Cyperaceae

Carex amphiloba Steud. CARIC SEDGE
Wet depressions
Carex cephalophora Muhl. CARIC SEDGE
Roadside depressions
Carex cherokeensis Schwein. CARIC SEDGE
Roadsides
Carex crus-corvi Ktze. CROW-FOOT SEDGE
Roadsides, open areas
Carex flaccosperma Dew. CARIC SEDGE
Wet depressions
Carex hyalinolepis Steud. CARIC SEDGE
Roadsides
Carex tribuloides Wahl. CARIC SEDGE
Wet depressions
Cladium jamaicense Crantz SAW-GRASS
Marshes
Cyperus elegans L. FLAT SEDGE
Roadsides
Cyperus erythrorhizos Muhl. FLAT SEDGE
Roadsides
Cyperus esculentus L. YELLOW NUT-GRASS
Open roadsides and wet depressions
Cyperus hermaphroditus (Jacq.) Standl. FLAT SEDGE
Wet depressions
Cyperus iria L. FLAT SEDGE
Wet depressions
Cyperus ochraceus Vahl FLAT SEDGE
Wet depressions
Cyperus odoratus L. FLAT SEDGE
Roadsides
Cyperus oxylepis Steud. FLAT SEDGE
Wet depressions

Cyperus strigosus L. FLAT SEDGE
Wet depressions
Cyperus virens Michx. SWAMP SEDGE
Wet depressions
Eleocharis cellulosa Torr. SPIKE-RUSH
Wet ground
Eleocharis macrostachya Britt. SPIKE-RUSH
Marshes
Eleocharis microcarpa Torr. SPIKE-RUSH
Wet ground
Eleocharis montevidensis Kunth SPIKE-RUSH
Roadsides
Rhynchospora corniculata (Lam.) Gray HORNED-RUSH
Wet areas, marsh edges
Scirpus californicus (Mey.) Steud. GIANT BULRUSH
Marshes
Scirpus cyperinus (L.) Kunth BULRUSH
Marshes, wet ground
Scirpus lineatus Michx. BULRUSH
Trailsides, hardwood bottoms

Palmae

Sabal minor (Jacq.) Pers. PALMETTO, LATANIER, PALMIER NAIN
Hardwood bottoms

Araceae

Arisaema dracontium (L.) Schott GREEN DRAGON
Hardwood bottoms
Colocasia antiquorum (L.) Schott ELEPHANT'S-EAR
Wet depressions, edges of bayous
Pistia stratiotes L. WATER-LETTUCE
Floating aquatic

Lemnaceae

Lemna minor L. DUCK-WEED
Floating aquatic
Spirodela polyrhiza (L.) Schleid. GREATER DUCK-WEED, DUCK-MEAT
Floating aquatic
Wolffia columbiana Karst. WATER-MEAL
Floating aquatic

Bromeliaceae

Tillandsia usneoides (L.) L. SPANISH-MOSS, BARBE ESPAGNOLE, MOUSSE D'ARBRE
Epiphyte

Commelinaceae

Commelina diffusa Burm. f. DAY-FLOWER
Roadsides
Commelina erecta L. WIDOW'S-TEARS
Roadsides, hardwood bottoms

Commelina virginica L. WIDOW'S-TEARS, DAY-FLOWER
Roadsides
Tradescantia ohiensis Raf. SPIDERWORT
Hardwood bottoms

Pontederiaceae

Eichhornia crassipes (Mart.) Solms WATER-HYACINTH
Floating aquatic
Pontederia cordata L. PICKEREL-WEED
Wet depressions

Juncaceae

Juncus effusus L. COMMON RUSH, SOFT RUSH
Wet depressions
Juncus tenuis Willd. SLENDER RUSH
Roadsides, wet depressions

Liliaceae

Allium canadense L. WILD ONION, ONION MARRON
Roadsides, hardwood bottoms
Nothoscordum bivalve (L.) Britt. FALSE-GARLIC
Roadsides
Smilax bona-nox L. CAT-BRIAR, SMILACE
Vine in hardwood bottoms, roadsides
Smilax hispida Muhl. CAT-BRIAR
Vine in hardwood bottoms
Smilax rotundifolia L. GREEN-BRIAR
Vine in hardwood bottoms, trailsides

Amaryllidaceae

Hymenocallis occidentalis (Le Conte) Kunth SPIDER-LILY, PANCRAIS
Wet depressions, marshes

Iridaceae

Iris fulva Ker. RED IRIS
Hardwood bottoms, occasional
Iris giganticaerulea Small GIANT BLUE IRIS
Open margins of swamps
Sisyrinchium rosulatum Michx. BLUE-EYED-GRASS
Trailsides in hardwood bottoms

Cannaceae

Canna flaccida Salisb. GOLDEN CANNA, INDIAN-SHOT
Wet depressions

Orchidaceae

Epidendrum conopseum R. Br. TREE ORCHID, GREEN-FLY ORCHID
Epiphyte in hardwood bottoms
Habenaria repens Nutt. WATER-SPIDER
Aquatic among water-hyacinth
Spiranthes cernua var. *odorata* (Nutt.) Correll FRAGRANT LADIES'-TRESSES
Occasional in open areas, trailsides.

Saururaceae

Saururus cernuus L. LIZARD'S-TAIL, PAGOGIE
Wet depressions

Salicaceae

Populus deltoides Marsh. COTTONWOOD, PEUPLIER LIARD
Hardwood bottoms
Salix nigra Marsh. BLACK WILLOW, SAULE
Hardwood bottoms, spoilbanks, disturbed areas

Myricaceae

Myrica cerifera L. WAX-MYRTLE, CIRIER
Trailsides and roadsides, marshes

Juglandaceae

Carya aquatica (Michx. f.) Nutt. WATER HICKORY
Swamp borders
Carya illinoinensis (Wang.) Koch PECAN
Hardwood bottoms

Fagaceae

Quercus nigra L. WATER OAK, CHÊNE
Hardwood bottoms
Quercus nuttallii Palmer NUTTALL OAK
Hardwood bottoms
Quercus virginiana Mill. LIVE OAK, CHÊNE
Hardwood bottoms, spoilbanks

Ulmaceae

Celtis laevigata Willd. HACKBERRY
Hardwood bottoms, disturbed areas
Ulmus americana L. AMERICAN ELM
Hardwood bottoms
Ulmus rubra Muhl. SLIPPERY ELM, ORME GRAS
Hardwood bottoms

Moraceae

Morus rubra L. RED MULBERRY
Trailsides in hardwood bottoms

Urticaceae

Boehmeria cylindrica (L.) Sw. FALSE NETTLE, ORTIE
Roadsides
Pilea pumila (L.) Gray CLEAR-WEED
Hardwood bottoms
Urtica chaemaedryoides Pursh NETTLE, ORTIE ROUGE
Hardwood bottoms

Viscaceae

Phoradendron tomentosum (DC.) Gray MISTLETOE
Parasitic epiphyte, hardwood bottoms

Polygonaceae

Brunnichia ovata (Walt.) Shinners EARDROP, ANSERINE LIANE
Vine in hardwood bottoms
Persicaria densiflora (Meisn.) Moldenke
Roadsides

Persicaria hydropiperoides (Michx.) Small
Roadsides, wet areas
Persicaria punctata (Ell.) Small SMART-WEED, CURAGE
Roadsides, wet areas
Persicaria setacea (Baldw.) Small
Roadsides
Polygonum ramosissimum Michx. KNOT-WEED
Roadsides
Polygonum virginianum L. JUMP-SEED
Hardwood bottoms
Rumex crispus L. YELLOW DOCK, PATIENCE
Roadsides
Rumex pulcher L. FIDDLE DOCK
Roadsides
Rumex verticillatus L. SWAMP DOCK
Roadsides, spoilbanks

Amaranthaceae

Acnida cuspidata Spreng. SOUTHERN WATER-HEMP
Disturbed areas
Alternanthera philoxeroides (Mart.) Griseb. ALLIGATOR-WEED
Swamps and margins of bayous

Phytolaccaceae

Phytolacca americana L. POKEWEED, CHOU GRAS
Roadsides
Rivina humilis L.
Spoilbanks

Portulacaceae

Portulaca oleracea L. PURSLANE
Wet depressions

Caryophyllaceae

Cerastium glomeratum Thuill. MOUSE-EAR
Trailsides, hardwood bottoms
Stellaria media (L.) Cyril. CHICK-WEED
Trailsides, hardwood bottoms

Cabombaceae

Cabomba caroliniana Gray FANWORT
Aquatic

Nymphaeaceae

Nymphaea odorata Ait. WHITE WATER-LILLY
Aquatic

Ceratophyllaceae

Ceratophyllum demersum L. COON-TAIL
Submerged aquatic

Ranunculaceae

Clematis crispa L. LEATHER-FLOWER
Hardwood bottoms, roadsides

Clematis ternifolia DC. JAPANESE VIRGIN'S-BOWER
Margins of hardwood bottoms
Ranunculus platensis Spreng.
Wet areas
Ranunculus pusillus Poir. BUTTERCUP
Roadsides
Ranunculus sceleratus L. BUTTERCUP
Margins of bayous
Ranunculus trilobus Desf. BUTTERCUP
Hardwood bottoms
Thalictrum dasycarpum var. *hypoglaucum* (Rydb.) Boiv. PURPLE MEADOW-RUE
Hardwood bottoms

Lauraceae

Cinnamomum camphora (L.) Nees & Eberm. CAMPHOR-TREE
Occasional in hardwood bottoms
Persea borbonia (L.) Spreng. RED BAY, LAURIER
Hardwood bottoms

Papaveraceae

Argemone albiflora Hornem. WHITE PRICKLY POPPY, PAVOT EPINÉUX
Shell beaches

Cruciferae

Cardamine pensylvanica Muhl. BITTER-CRESS
Hardwood bottoms
Lepidium virginicum L. PEPPERWORT, CRESSON
Roadsides

Hamamelidaceae

Liquidambar styraciflua L. SWEET GUM, RED GUM, COPAL
Hardwood bottoms

Rosaceae

Crataegus viridis L. GREEN HAW
Hardwood bottoms
Duchesnea indica (Andrz.) Focke INDIAN STRAWBERRY
Hardwood bottoms
Geum canadense Jacq. WHITE AVENS
Hardwood bottoms, trailsides
Rubus trivialis Michx. DEWBERRY, RONCE
Roadsides and open areas

Leguminosae

Acacia smallii Isely ACACIA, HUISACHE, OPOPANAX
Shell beaches
Aeschynomene indica L. JOINT VETCH
Roadsides, wet areas
Cassia fasciculata Michx. PARTRIDGE PEA
Open areas, roadsides
Centrosema virginianum (L.) Benth. BUTTERFLY PEA
Open areas

Desmanthus illinoensis (Michx.) Macm. PRAIRIE MIMOSA
Disturbed areas
Desmodium canescens (L.) DC. BEGGAR'S-TICKS
Open areas
Desmodium glabellum (Michx.) DC. BEGGAR'S-TICKS
Open areas
Desmodium laevigatum (Nutt.) DC. BEGGAR'S-TICKS
Open areas
Desmodium paniculatum (L.) DC. BEGGAR'S-TICKS
Open areas
Gleditsia triacanthos L. HONEY-LOCUST, EPINE DE LA PASSION
Hardwood bottoms
Melilotus indicus (L.) All. YELLOW SOUR CLOVER
Roadsides
Mimosa strigillosa Torr. & Gray. POWDER-PUFF
Disturbed areas
Pueraria lobata (Willd.) Ohwi KUDZU
Roadside vine
Rhynchosia minima (L.) DC. SNOUT-BEAN
Roadsides
Sesbania macrocarpa Muhl. COFFEE-BEAN, INDIGOTIER
Roadsides
Sesbania punicea (Cav.) Benth. RED RATTLEBOX
Roadsides
Strophostyles helvola (L.) Ell. WILD BEAN
Roadsides
Trifolium repens L. WHITE CLOVER
Trailsides, hardwood bottoms
Trifolium resupinatum L. PERSIAN CLOVER
Open areas
Vicia ludoviciana Nutt. VETCH
Open areas and trailsides
Vigna luteola (Jacq.) DEER PEA, WILD COW PEA
Marshes, open areas

Geraniaceae

Geranium carolinianum L. WILD GERANIUM
Open disturbed areas

Oxalidaceae

Oxalis corymbosa DC.
Hardwood bottoms
Oxalis dillenii Jacq. WOOD SORREL
Roadsides and trailsides

Rutaceae

Citrus sp. CITRUS
Occasional in hardwood bottoms, escaped from cultivation

Meliaceae

Melia azedarach L. CHINABERRY
Occasional at roadsides

Euphorbiaceae

Acalypha rhomboidea Raf. THREE-SEEDED MERCURY
Roadsides
Euphorbia cordifolia Ell. SPURGE
Roadsides
Euphorbia hirta L. SPURGE
Disturbed areas
Euphorbia nutans Lag. SPURGE
Disturbed areas
Euphorbia prostrata Ait. SPURGE, MAL NOM
Roadsides
Euphorbia supina Raf. SPURGE
Disturbed areas
Phyllanthus urinaria L. LEAF-FLOWER
Roadsides
Sapium sebiferum (L.) Roxb. CHINESE TALLOW-TREE
Roadsides and spoilbanks

Anacardiaceae

Rhus toxicodendron var. *vulgaris* Michx. POISON-IVY
Vine in hardwood bottoms and disturbed areas

Aquifoliaceae

Ilex decidua Walter POSSUM-HAW
Hardwood bottoms
Ilex vomitoria Ait. YAUPON
Hardwood bottoms, spoilbanks

Aceraceae

Acer negundo L. BOX-ELDER, BOIS PANT
Hardwood bottoms
Acer rubrum var. *drummondii* (H. & A.) Sarg. SWAMP RED MAPLE, ERABLE
Hardwood bottoms

Sapindaceae

Cardiospermum halicacabum L. BALLOON-VINE, POIS DE MERVEILLE
Roadsides
Koelreuteria paniculata Laxman GOLDEN RAIN-TREE
Roadsides

Rhamnaceae

Berchemia scandens (Hill) Koch SUPPLE-JACK
Vine in hardwood bottoms

Vitaceae

Ampelopsis arborea (L.) Koehne PEPPER-VINE
Vine in hardwood bottoms
Ampelopsis cordata Michx.
Vine in hardwood bottoms

Parthenocissus quinquefolia (L.) Planch. VIRGINIA CREEPER
Vine in hardwood bottoms
Vitis cinerea Engelm. GRAYBARK GRAPE
Hardwood bottoms
Vitis rotundifolia Michx. MUSCADINE
Hardwood bottoms

Malvaceae

Hibiscus lasiocarpus Cav. ROSE-MALLOW
Marshes, roadsides, wet depressions
Kosteletzkya virginica (L.) Gray SALT-MARSH MALLOW
Swamp margins, spoilbanks, wet depressions
Malvastrum coromandelianum (L.) Garcke
Hardwood bottoms
Modiola caroliniana (L.) G. Don MAUVE, GUIMAUVE
Roadsides
Sida rhombifolia L. GUMBO DE ST. JEANNE
Open areas

Hypericaceae

Ascyrum hypericoides L. ST. ANDREW'S CROSS, HERBE À CHIEN
Roadsides
Hypericum walteri Gmel. ST. JOHN'S-WORT, MILLEPERTUIS
Open areas

Violaceae

Viola papilionacea Pursh VIOLET, VIOLETTE MARONNE
Hardwood bottoms
Viola septemloba Le Conte VIOLET
Open areas

Passifloraceae

Passiflora incarnata L. MAYPOP
Vine in open areas
Passiflora lutea L. YELLOW PASSION-FLOWER, LIEN À VIPÈRE
Vine in open areas

Lythraceae

Ammannia coccinea Rottb. TOOTH-CUP
Roadsides
Cuphea carthagensis (Jacq.) Macbr.
Roadsides
Lythrum lanceolatum Ell. LOOSESTRIFE, HERBE À BALE
Roadsides

Onagraceae

Ludwigia decurrens Walt. PRIMROSE-WILLOW
Open wet depressions
Ludwigia leptocarpa (Nutt.) Hara WATER-PRIMROSE
Edges of bayous
Ludwigia octovalvis (Jacq.) Raven WATER-PRIMROSE, SEEDBOX
Roadsides

Ludwigia uruguayensis (Camb.) Hara
Marshes
Oenothera speciosa Nutt. MEXICAN PRIMROSE

Umbelliferae

Chaerophyllum tainturieri Hook. CHERVIL
Hardwood bottoms
Cicuta mexicana Coult. & Rose WATER-HEMLOCK
Roadsides in wet depressions
Hydrocotyle ranunculoides L. f. PENNYWORT
Wet areas
Hydrocotyle umbellata L. MARSH PENNYWORT
Margins of swamps and marshes
Hydrocotyle verticillata Thunb. PENNYWORT, GOBELET
Wet areas
Lilaeopsis carolinensis C. & R.
Wet areas
Ptilimnium capillaceum (Michx.) Raf. MOCK BISHOP'S-WEED
Trailsides and marshes
Sanicula canadensis L. BLACK SNAKEROOT
Trailsides

Cornaceae

Cornus drummondii Mey. ROUGH-LEAF DOGWOOD
Roadsides, margins of hardwood bottoms
Nyssa aquatica L. WATER TUPELO
Swamps

Primulaceae

Anagallis arvensis L. SCARLET PIMPERNEL, MOURON
Roadsides
Samolus parviflorus Raf.
Hardwood bottoms

Sapotaceae

Bumelia lycioides (L.) Pers. IRONWOOD
Shell beaches

Ebenaceae

Diospyros virginiana L. PERSIMMON, PLAQUEMINIER
Hardwood bottoms, trailsides, spoilbanks

Oleaceae

Fraxinus caroliniana Mill. CAROLINA ASH, WATER ASH
Hardwood bottoms
Fraxinus pensylvanica Marsh. RED ASH, FRÊNE GRAS
Hardwood bottoms
Fraxinus profunda (Bush) Bush PUMPKIN ASH
Swamp and marsh borders
Ligustrum japonicum Thunb. PRIVET
Hardwood bottoms, escaped from cultivation
Ligustrum lucidum Ait. PRIVET
Hardwood bottoms, escaped from cultivation

Loganiaceae

Cynoctonum mitreola (L.) Britt. MITREWORT
Roadsides and trailsides

Gentianaceae

Sabatia calycina (Lam.) Heller ROSE-GENTIAN
Hardwood bottoms

Asclepiadaceae

Asclepias perennis Walt. MILKWEED
Margins of hardwood bottoms
Matelea gonocarpa (Walt.) Shinners VACHE A LÀIT
Trailside vine in hardwood bottoms

Convolvulaceae

Dichondra carolinensis Michx.
Hardwood bottoms
Ipomoea x *leucantha* Jacq.
Roadsides
Ipomoea trichocarpa Ell. MORNING-GLORY, LISERON
Roadsides
Ipomoea sagittata Cav. MORNING-GLORY
Marshes

Hydrophyllaceae

Nemophila aphylla (L.) Brum. BABY BLUE-EYES
Hardwood bottoms

Boraginaceae

Heliotropium curassavicum L. SEASIDE HELIOTROPE
Wet depressions
Lithospermum tuberosum A. DC. GROMWELL
Hardwood bottoms, trailsides
Myosotis macrospermum Engelm. FORGET-ME-NOT
Hardwood bottoms

Verbenaceae

Callicarpa americana L. FRENCH-MULBERRY, CHASSEPAREILLE
Hardwood bottoms
Phyla nodiflora (L.) Greene FROG-FRUIT
Wet areas
Verbena brasiliensis Vell. BRAZILIAN VERVAIN
Roadsides, disturbed areas
Verbena rigida Spreng. VERVAIN
Roadsides
Verbena urticifolia L. WHITE VERVAIN
Roadsides

Labiatae

Lycopus rubellus Moench BUGLE-WEED
Swamps
Lycopus virginicus L. BUGLE-WEED
Hardwood bottoms
Salvia coccinea Murr. RED SAGE
Disturbed areas

Stachys crenata Raf. SHADE BETONY
Disturbed areas
Stachys tenuifolia Willd. HEDGE-NETTLE
Hardwood bottoms, trailsides

Solanaceae

Petunia parviflora Juss. WILD PETUNIA
Roadsides
Physalis angulata L. GROUND CHERRY, COQUERET
Roadsides
Solanum americanum Mill. NIGHTSHADE, MORELLE
Disturbed areas
Solanum carolinense L. HORSE-NETTLE, TOMATE MARRONNE
Disturbed areas

Scrophulariaceae

Agalinis purpurea (L.) Penn.
Roadsides
Bacopa monnieri (L.) Wettst. WATER-HYSSOP
Wet depressions
Mazus japonicus (Thunb.) Ktze.
Open areas
Mecardonia acuminata (Walt.) Small CHELONE
Wet areas, roadsides
Mecardonia procumbens (Mill.) Small
Roadsides
Mimulus alatus Ait. MONKEY-FLOWER
Hardwood bottoms
Veronica peregrina L. SPEEDWELL
Roadsides
Veronica persica Poir. PERSIAN SPEEDWELL
Roadsides

Bignoniaceae

Bignonia capreolata L. CROSS-VINE
Hardwood bottoms
Campsis radicans (L.) Seem. TRUMPET-CREEPER, HERBE À PUCE
Hardwood bottoms

Lentibulariaceae

Utricularia gibba L. BLADDERWORT
Marshes

Acanthaceae

Dicliptera brachiata (Pursh) Spreng.
Open areas
Hygrophila lacustris (Schl. & Cham.) Nees
Wet depressions
Justicia lanceolata (Chapm.) Small WATER-WILLOW
Hardwood bottoms
Ruellia nudiflora (Gray) Urban
Disturbed areas

Plantaginaceae

Plantago major L. PLANTAIN
Roadsides

Rubiaceae

Cephalanthus occidentalis L. BUTTON-BUSH, BOIS DE MARAIS
Hardwood bottoms
Diodia virginiana L. BUTTON-WEED
Roadsides
Galium aparine L. BEDSTRAW
Roadsides and trailsides
Galium tinctorium L. BEDSTRAW
Hardwood bottoms

Caprifoliaceae

Lonicera japonica Thunb. JAPANESE HONEYSUCKLE
Vine in open areas
Sambucus canadensis L. ELDERBERRY, SUREAU
Roadsides, spoilbanks

Cucurbitaceae

Cucurbita texana Gray TEXAS GOURD
Open areas
Melothria pendula L.
Roadsides

Lobeliaceae

Lobelia cardinalis L. CARDINAL FLOWER
Hardwood bottoms

Compositae

Ambrosia artemisiifolia L. RAG-WEED
Disturbed areas
Ambrosia psilostachya DC. RAG-WEED
Disturbed areas
Ambrosia trifida L. GIANT RAG-WEED
Roadsides
Aster lateriflorus (L.) Britt. WHITE ASTER
Roadsides, spoilbanks
Aster praealtus Poir. BLUE ASTER
Roadsides
Aster subulatus var. *ligulatus* Shinners
Roadsides
Baccharis halimifolia L. BUCKBUSH, MANGLIER
Roadsides, spoilbanks
Bidens bipinnata L. SPANISH-NEEDLES
Open areas
Bidens laevis (L.) BSP. BUR-MARIGOLD
Swamp margins
Cirsium horridulum Michx. BULL THISTLE, CHOUDRONS
Margins of hardwood bottoms

Eclipta alba (L.) Hassk. SOUCI
Roadsides
Erigeron philadelphicus L. FLEABANE, DAISY MARRONNE, VERGEROLLE, HERBE À VERS
Disturbed areas
Elephantopus carolinianus Raeusch. ELEPHANT'S-FOOT
Roadsides and trailsides
Eupatorium capillifolium (Lam.) Small DOG-FENNEL, ANIS MARRON
Roadsides
Eupatorium coelestinum L. MIST-FLOWER, TÊTE DE FEMME BLEUE
Roadsides
Eupatorium rugosum Houtt. WHITE SNAKEROOT, TÊTE DE VIELLE FEMMES
Disturbed areas
Eupatorium serotinum Michx. BONESET
Open areas
Iva annua L. MARSH-ELDER, SWAMP-WEED
Roadsides. wet areas
Lactuca canadensis L. WILD LETTUCE, LAITUE
Open areas, spoilbanks
Lactuca floridana (L.) Gaertn. WILD LETTUCE
Open areas
Mikania scandens (L.) Willd. HEMP-WEED
Roadsides
Parthenium hysterophorus L. FALSE RAG-WEED
Roadsides
Pluchea odorata (L.).Cass. CAMPHOR-WEED, BAUME DES SAUVAGES
Open areas
Polymnia uvedalia (L.) L. BEAR'S-FOOT
Margins of hardwood bottoms
Pyrrhopappus carolinianus (Walt.) DC. FALSE DANDELION
Roadsides
Senecio glabellus Poir. BUTTER-WEED
Wet areas
Solidago altissima L. GOLDENROD, VERGE D'OR
Roadsides
Solidago sempervirens L. SEASIDE GOLDENROD
Open areas, wet depressions
Spilanthes americana (Mutis) Hieron.
Trailsides in hardwood bottoms
Verbesina virginica L. FROST-WEED, HERBE À TROIS QUARTS
Open areas
Vernonia gigantea (Walt.) Trel. ex Bran. & Cov. IRON-WEED
Open areas
Xanthium strumarium L. COCKLEBUR
Trailsides
Youngia japonica (L.) DC.
Disturbed areas

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